

ANALYSIS OF THE ANIMAL COMMUNITY IN A BEECH FOREST FLOOR

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CHAPTER I

INTRODUCTION.

The forest is one of the most complex communities we know. Trees, bushes, herbs and mosses are the easily perceptible botanical components of this community. Moulds, bacteria, algae and other lower plants are mostly less conspicuous, but play such a prominent part in the community that it could not exist without their presence.

The animal components of this community are less striking still. Nevertheless all phyla of the Animal Kingdom tied to a terrestrial life are represented in the community of the forest. The animal community, like the vegetable, is composed of species of greatly diverging sizes. Mammals and birds are the biggest representatives of the fauna in the community, Protozoa the smallest. Between them there is a continuous spectrum of sizes.

Whereas, however, it is relatively easy to analyse the larger elements of the vegetable community quantitatively, this is not the case with the majority of the elements of the animal community. Mobility and a hidden way of living greatly interfere with the quantitative investigation, while the fact that animals only temporarily form part of the community and fluctuate in numbers during the course of the year necessitates reinvestigation with certain intervals.

From the abundance of animal species it is inevitable that a thorough investigation into the animal community of a forest should only be practicable by the collaboration of a number of research workers each of whom occupies himself with a special part of the community. Methods of investigation must be such that the results can be synthesized.

The division of the investigation into the community can take place in several ways. It can be based on different systematic units: by collaboration of an ornithologist, some entomologists, a malacologist and other specialists a great part of the fauna can be investigated. An objection is that nearly always some groups that are of great importance in the community e.g. Nematoda and Oligochaeta are not taken into account by lack of specialists, while on the other hand a disproportionate amount of detail-work is done on groups that are of more interest to systematists or autecologists but that are of secondary importance to the knowledge of the cycle in the community.

Another principle for division of the investigation into the community is that based on the direct relation between elements of the community. Examples are: phytophagous insects and their natural enemies, ants and plant-lice, birds and their prey-insects living in the soil, in the trunks and on the leaves, the fungivorous fauna in the soil and the moulds in the dead organic material etc. These relations are still unknown to a great extent, however. Many observations on living animals, data of breeding and extensive literature research are necessary to increase our knowledge in this respect.

A third method of division of community investigation can be

based on objective quantitative methods of collecting each of which concerns one, or usually more systematic units, the errors of which for the different species are known. With a complete set of these methods it will be possible to get an insight into the qualitative and quantitative composition of the fauna.

These methods of collecting should in the first place be focussed on the quantitative analysis of the fauna of a certain merotope. By this term we understand with MÖRZER BRUYNS (1947) a more or less independent part of a biotope, occurring in the forest as top layer, trunk layer, herbaceous layer, moss layer, litter layer and soil layer (stratotopes) or as parts with differing ecological circumstances of their own: mouldered tree stumps, left and occupied ant hills, excrements of larger mammals, nests of birds and so on.

The quantitative collecting in a certain stratotope can be done best by examination of random-tests, the size of which is in proportion to the size and the density of the species concerned. In practice only species with a fairly large density can be used. For species that occur in a small density the samples have to be taken either too large or in too great a number to get still workable data. Mostly these less abundant species play a subordinate part in the economics of the community so that the lack of exact data of these species influences the total proportions but slightly.

In general random-samples of a certain volume or surface which are examined on their live-stock in the laboratory appear to satisfy best for quantitative work.

BASKINA and FRIEDMANN (1928) compared catches with a field-photoclector with net catches in isolated surfaces in a meadow biotope and found the highest catches with the latter method. In an investigation of the top fauna the best results are got by branches isolated in bags (PALMGREN 1932).

As to the abundant species the fauna of the soil can be best investigated quantitatively in samples of a certain volume as will be explained in chapter III.

The investigation into the animal community in the forest, its influence in the biocoenosis of the forest and the regulation of the members of its components is one of the most important points of the program of the "Institute for Biological Field Research T.N.O."

Since the foundation of this institute in 1940 insect pests in forests are studied especially from the aspect of disturbances of the balance in the natural community.

The investigation of BESEMER (1942) into the dispersal and regulation of the pest of *Diprion pini* L. in the years 1938—1940 brought to light an important influence of the fauna of the soil on this pest. Hence from the beginning the investigation into the fauna of the soil has been on the working program of the institute.

Investigations were made into the composition of the ant fauna in various forest types (QUISPEL 1941, WESTHOFF and WESTHOFF-DE JONCHEERE 1942).

An investigation into the fauna of mice was made (not published).

In 1940—1941 NOORDAM and VAN DER VAART-DE VLIENER made an investigation into the litter fauna of a rather natural forest of oaks and birches limited to the youngest generation of litter. The fauna was investigated during the course of one year and the most important species bred in the laboratory and investigated into their food (NOORDAM and VAN DER VAART-DE VLIENER 1943). In this investigation the importance of the litter fauna for the decomposition of the litter was accentuated.

In 1942 Miss Dr M. ROOSEBOOM and the author were charged with the investigation of the forest soil. After continuation of the series of the examinations of NOORDAM and VAN DER VAART at first, the investigation was given another turn. The investigation of the fauna of one generation of litter causes many difficulties: the separation of two adjacent layers is often hard to effect. Owing to the vertical migration of the fauna the population of one layer is greatly affected by the population of the layers above and below, so that for a better understanding the whole layer of litter and humus has to be investigated.

Up till 1945, the time she was attached to the institute, Dr ROOSEBOOM made breeding experiments in the laboratory to get data, as to the way of feeding, the reproduction, the rapidity of development, term of life etc. of the quantitatively important species.

The field research, the author was charged with, had in view the composition of the animal community in forest soil. This investigation could continue the technique used by NOORDAM and VAN DER VAART-DE VLIENER, BORNEBUSCH (1930), TRÄGÅRDH and FORSSLUND (1932), and ULRICH (1933), who all used the desiccation technique of BERLESE modified by TULLGREN (1917); when this method yielded bad results for certain groups of animals, other methods were applied: immersing technique, and trap technique. With the aid of methods complementing each other the whole fauna of litter can be studied quantitatively. Unfortunately the study of some groups had to remain less detailed for lack of specialists in identifying species.

The investigation, the results of which will be given and discussed here, was made in an 80 years' old forest of beeches on rather poor diluvial sandy soil at Hoenderloo (about 14 km north of Arnhem), with a layer of litter and humus of 4-10 cm high and without any undergrowth. A description of this forest, its humus layer and its direct environments will be given in chapter IV.

The reasons why this investigation was made in this very uniform forest are the following: because of the absence of any herb or moss vegetation in the greater part of the forest the fauna of the floor is a pure litter fauna, in which no elements occur that are dependent on moss vegetation and roots of herbs. Moreover it was expected that in this uniform floor the composition of the fauna would be as homogeneous as possible, which is of great value in an investigation into the seasonal fluctuations and in general in any investigation where parallel samples are desirable. Finally the results tell us the composition of the fauna in the floor of a forest with a

slow decomposition of the organic material which for that reason asks the interest of economic forestry. It is in these very forests where the decomposition of the litter should be accelerated, by interfering into the soil fauna under certain circumstances. However, before we are able to deal with this practical matter we ought to be acquainted with the composition and the way of living of the autochthonous fauna. Only when this is the case we can perhaps try to promote those species that have a favourable effect on the decomposition, but that now could not have an important influence because of their small density.

After a summary of the literature of the fauna of forest soil (chapter II) the methods for the quantitative investigation will be discussed in detail (chapter III). In chapter IV a description will be given of the forest investigated as the environment for the soil fauna and of some climatic conditions there. The animal community itself will be described and discussed in chapter V. At last in chapter VI the importance of the soil fauna for the decomposition of the litter will be discussed.

At the performance of the investigation and at the preparation of this paper much help was given by several persons. At first I am much indebted to Prof. Dr C. J. VAN DER KLAUW for his continuous interest and his most helpfull criticism. Also the advices and stimulant remarks of the director of the institute Dr A. D. VOÛTE have contributed much to the results of the investigation. I regret that the very pleasant cooperation with Dr M. ROOSEBOOM had to be finished in 1945 already. Many of her breeding results are referred to in the special part of Chapter V A. For the translation of the manuscript and the laborious correction-work I wish to express my sincerest thanks to Miss M. M. C. VON DER MÖHLEN and to my wife.

Though in general the identifications of the species were performed by myself, for informations and control of my identifications much help was given by specialists to whom I render my best thanks in this place also. In particular I should like to mention Miss A. M. BUITENDIJK †, Leiden (Collembola) and Messrs. W. BOELEN, Hengelo (Staphylinidae), Dr H. C. BLÖTE, Leiden (Hemiptera), G. L. VAN EYNDOVEN, Haarlem (Acari), L. VAN DER HAMMEN, Leiden (Arachnoidea), C. A. W. JEEKEL, Amsterdam (Myriapoda), Dr C. DE JONG, Leiden (Coleoptera), Prof. Dr J. C. H. DE MEIJERE †, Amsterdam (Diptera larvae), D. PIET, Amsterdam (Diptera) and C. WILLEMSE, Eysgelshoven (Orthoptera).

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CHAPTER II

THE CONCEPT "SOIL FAUNA" AND A SURVEY OF
THE LITERATURE CONCERNING THE
FAUNA OF FOREST SOIL

Before we pass in review the most important literature on this subject it seems useful to give some attention to the concepts "soil" — especially "forest soil" — and "soil fauna".

Here we understand by soil the mineral substrate in which the vegetation takes root, including the dead organic material, which is found both in and upon the mineral substrate.

Dependent on the kind of the decomposition of the organic material falling on the soil surface every year, there arise greatly different types of forest soils. In consequence of a quick decomposition of the litter, chiefly under the influence of bacteria, corrosive fungi (which attack both cellulose and lignin), and a rich macrofauna, a so called "mull-type" arises in which the pH is rather high, the humus is entirely mixed with the mineral substance and the latter has a crumbly structure. In consequence of a slow decomposition the litter accumulates on the mineral substance: destructive fungi attack to some degree cellulose, but not lignin, and form organic acids; with the low pH bacteria play a subordinate part only and the fauna is chiefly represented by small animals (mesofauna) which occur almost exclusively in the organic layers and so are not capable of mixing organic and inorganic substance. Neither do the small numbers of the bigger elements, likewise mainly restricted to the organic layers. This type of soil, composed of fairly distinct layers of litter, humus and mineral soil is called "mor-type". Organic acids and humus substances, washed away from the humus layer, cause leaching of the upper layers of the mineral underground.

Concerning the soil fauna it is important to fix how far the concept extends. Should we understand by it all animals that influence the soil by their activity in any period of their life, nearly all terrestrial animals ought to come under this head. Should we, on the other hand, understand by it only those animals that spend their whole life in the soil then we should exclude a great number of animals that only during their larva or cocoon stage inhabit the soil.

The most simple and satisfying definition of the soil fauna is: those animals that occur in the soil either during their whole life or in one or more of their developmental stages. If a species only spends a part of its life in the soil then only this stage is considered to belong to the soil fauna.

To perform certain vital functions such as reproduction, feeding and dispersion many animals of the soil come temporarily to the surface of the soil: millipedes, earthworms, groundbeetles etc. Winged species are even able to leave the surface of the soil for some time for the sake of reproduction (ants) or to reach food (dungbeetles, burying beetles). The interruption of the contact with

the soil is of too short a duration however, to take this stage not completely into the soil fauna.

The fauna of the soil defined in this way can be divided into a number of groups on different principles.

As a first distinguishing mark, the size of the animals can be used. FENTON (1947) distinguished the soil fauna into micro-, meso- and macrofauna, the distinction of which he takes at 40 μ and some centimetres. To the division of the fauna into these three groups of size and the limits we take for them, we will return in chapter III in discussing the sampling technique.

If we take the occurrence in the soil during the different stages of life we can distinguish with JACOT (1940):

1. geobiontic species viz. those species that spend their whole cycle of life i.e. from egg to egg, in the soil: earthworms, millipedes, many mites and collembolae etc.
2. geophilous species, spending only part of their life cycle in the soil e.g. larvae of many Diptera, wireworms, cocoons of moths, hibernating imagines of some bugs, beetles etc.

Apart from the occurrence in the soil which depends on what an organism in its different stages requires of its environment it seems useful to distinguish the fidelity of an organism (geobiont) or stage of an organism (geophile) to the soil, dependent on the fact in what degree the soil as environment fulfils the requirements of a species or stage. In accordance to phyto-ecology, denoting the degrees of the fidelity of a species to a certain plant community with the terms exclusive, selective, preferent and indifferent we will use the same terms (with omission of the second) for the fidelity of a species to a certain merotope as habitat¹), with about the same limitations. To these terms we will add the term „subferent”, indicating those species, that are preferent in other merotopes.

If the soil exclusively fulfils the requirements of a species, the latter is not able to live away from this merotope and the highest degree of fidelity is given: the species is an exclusive soil inhabitant. If in any other merotope e.g. in tree stumps or on tree bark the requirements to some degree are fulfilled, the species is also able to live here but it shows preference for the soil as habitat. In this case the species has a lower degree of fidelity to the soil and may be called a preferent soil inhabitant. If no preference is shown for the soil, as the requirements are fulfilled in the same degree in any other merotope, the species can be called an indifferent soil inhabitant. Subferent soil inhabitants are those species that are preferent in other merotopes. Geoxenes, finally, are animals that in consequence of some cause or other have strayed into the soil but do not belong here (JACOT 1940).

To determine the degree of fidelity it is necessary to know exactly the environmental requirements of the species (stage) and the environmental conditions of the merotope concerned. This requires

¹) habitat used in the same sense as MÖRZER BRUYN (1947) does: area occupied by an organism (or by a coenosis).

a thorough investigation both of the species and of the merotope. The fulfilment of the species requirements by the merotope is reflected in a high degree by abundance and frequency of the species. So these characteristics of a species in all environments that offer the possibility of living, give a rather good impression of the fidelity of the species to a certain merotope. In this respect we have a thorough knowledge of few species only.

The concept fidelity can also be applied to the preference of a species (stage) for a certain stratum in the forest soil. Several species of mites for example inhabit exclusively the top layer of litter, others the humus layer, most of them, however, are preferent inhabitants of the deeper layer of litter. That with respect to layer preference the concept fidelity is only of limited value, appears in extreme circumstances such as great drought: many species leave their layer of preference, but repopulate it when normal circumstances return.

On this preference for certain layers though in broader sense, the classification of KRAUSSE (1929) is based. He distinguished in the edaphic community: the eudaphon, the inhabitants of the mineral soil; the hemiedaphon, the inhabitants of the litter and the epedaphon, the inhabitants of the surface of the soil. The hypere-daphon, the inhabitants of the low vegetation is not to be considered as belonging to the soil fauna unless perhaps as subferent inhabitants of the soil.

Another classification can be based on the numbers of individuals in which the species occur in the samples. In this classification the size of the species concerned plays an important part, since the number in which it occurs in a sample (abundance, density) and the dispersal of a species as this is expressed in percents of the total numbers of samples in which the species is present (frequency) must always relate to a living space (size of the sample) that has a real meaning for that species as there is a pregnant proportion between the average volume of the body of an individual and the living space, offering the individual the necessary food etc. So the volume of the samples has to be taken of a different size for each species with a different individual volume. In practice this is only possible for a group of species within a certain range of sizes. On these groups and their ranges of size I shall return in the chapters III and V.

For species of the same group of size the percentage of the samples in which each species is met with, the frequency percentage ($F\%$), gives an idea of the homogeneity of the dispersal of the species in the merotope examined. As to the density we can compare the species mutually through the quantities in which they occur on an average in a sample (absolute abundance) or through the percentages they form of the total number of animals present (relative abundance, dominance).

A last classification, clearly demonstrating the different functions of the elements of the soil community is based on food relations.

JACOT (1940) indicates animals dependent on parts of green

plants (phytophages) as primaries, animals feeding on dead plant material (saprophages) as low primaries. Animals in their feeding dependent on primaries (predators, parasitoids, parasites) are called secondaries, animals dependent on the latter tertiaries etc. Mould-eaters, carrion-eaters and dung-eaters he summarizes as low secondaries.

Especially direct food relations are important for an insight into the mutual relations between the elements of the community and those between these elements and their abiotic environment: phytophages, predators, fungivorous animals (mould-eaters), saprophages (detritus-eaters), coprophages (excrement-eaters), necrophages (carrion-eaters). I should like to add to it the aphages, animals that do not feed during their stay in the soil.

However, these indications have no more than a schematic value. Only very few species are restricted to one way of feeding; generally different food is eaten, dependent on the need and the supply of food.

In relation to the purpose of this study the following summary of the most important literature is confined to those investigations that concern the whole fauna of forest soil. So it is possible to trace superficially the historical development of the soil fauna research, the different methods employed, the varying extent of the investigations both to the animal groups considered and to the extent of sampling and the different aims of the investigators. Afterwards we shall try to gain some general views from the results and outline the purpose of the present investigation.

The first who made a complete investigation into the fauna of the soil was DIEM (1903) in his "Untersuchungen über die Bodenfauna in den Alpen".

A number of 86 samples in all was taken out of different biotopes including forests. He used samples of 25×25 cm to a depth agreeing with the depth of roots (of herbaceous plants?). The samples were sieved in a number of small parts on a sieve with a mesh size of 2 mm and the animals were stimulated to move by the smoke of tobacco. Nematodes, enchytraeids, lumbricids, and myriapods were counted and the species of the last two groups were identified. Of "the fauna of the soil in a broader sense", viz. species spending only part of their life in the soil, the larvae of beetles were counted but not identified. Of molluscs and collembolus the species were identified, of the mites only the total number was noted. Through the method of investigation — sieving mechanically, using loupe-magnification in counting — the smaller species (mites and collembolus occurring to maximally a few tens per sample in the forest soil!) are underestimated. Moreover one sample per biotope is insufficient for a mutual comparison of the results. The conclusions, as far as they concern the quantitative results, are consequently wholly unreliable.

In 1911 an introductory investigation into the fauna of German forest soil was published by RAMANN. He examined samples of

one liter taken to a depth of 11 cm with the unaided eye, so that only the numbers of larger animals found by him (he only mentions earthworms) have some value. His numbers of smaller animals of which he only mentions enchytraeids and nematodes, are due to his technique undoubtedly lower than in reality. Nevertheless, he forms a high estimate of the importance of the soil animals, especially in respect of the forming of humus and the mixing of organic parts in the soil. Aware of the introductory character of his work he urges a more thorough investigation.

It was not before 1922 that the quantitative investigation into the animal community in the forest soil was started with more modern methods. In that year in Bavaria an investigation into the composition of the litter fauna in pine woods was made by PILLAI (1922) and some years later v. PFETTEN (1925) made a similar investigation for spruce woods. The starting point of these investigations was the question of the meaning of the litter fauna in causing and preventing disturbances of the equilibrium leading to insect pests (ESCHERICH 1922). These investigations were executed on samples of 1 m², first sieved mechanically and then desiccated in an apparatus, described by TULLGREN in 1917 (see chapter III). Samples of such an extent yielded nematodes, collemboles, and mites in uncountable quantities. Of the larger animals the species were determined and their numbers were fixed. The small number of samples, however, resp. 24 and 12 originating moreover from different forests do not permit conclusions concerning seasonal fluctuations and quantitative differences in the fauna of different forests. The importance of the investigation is to be found in the proof furnished by it that great numbers of animals occur in the layer of litter. A quantitative investigation into the smaller forms (mites, collemboles, nematodes) can only be performed in considerably smaller samples. Of the larger forms which are expected to give rise to or prevent pests, either far greater numbers of samples should be examined, which is technically impracticable, or other methods should be developed to be able to study density, fluctuation, and phenology of these species.

GRIMMET (1926) made an investigation into the fauna of the soil in two primary forests in New Zealand: a beech forest and a tawa forest (*Beilschmiedia tawa*). The soil types are not exactly described but probably belong to the mull-type. From March up to September inclusive samples were examined in the two forests every month. The samples were composed of 10 small samples taken from several parts of the plot and had a total surface of about $\frac{1}{2}$ m². The whole of them was examined for the macrofauna, and $\frac{1}{8}$ part for smaller animals. In consequence of his direct method of investigating a great part of the smaller animals, no doubt, remained unobserved. Nematodes and collemboles for example were only found in very small numbers. The highest number of mites amounted to 640 per sample. As to the larger taxonomic groups, classes and orders, the qualitative composition of the litter fauna greatly agrees with the European; the genera

and species and partly even the families, however, are quite different.

In Czechoslovakia SOUDEK (1928) made an investigation into the fauna of a spruce wood, 50—70 years old, mixed with some scattered pines, larches and oaks. From September to April monthly samples of $\frac{1}{2}$ m² comprising the whole organic layer were taken and sieved in a Tullgren-apparatus. Collembolae and mites were estimated in hundreds, the other animals were counted. In consequence of his very large samples the numbers found for mites (2,800 — 12,300) and collembolae (650 — 19,400) are probably too low. As we shall see, relatively more animals dry up in larger samples than in smaller ones. Counting the catching results minutely is greatly hindered — if not made impossible — by vitiating organic parts and by the very large numbers of animals. Important are his estimates of the quantity of material passing the intestinal tract of the soil fauna. On account of the volume of the intestinal canal and supposing its contents passes twice in 24 hours, he calculates a daily production of excrements of 0.024 mm³ for collembolae, 0.005 mm³ for mites, and 0.75 mm³ for enchytraeids. He estimates that in the given circumstances the whole layer of litter would be decomposed by the fauna of the soil in 20 years (with a time of activity of 300 days a year). On these results we will return in chapter VI.

In the same year TRÄGÅRDH (1928) published a study on the fauna of the soil in the Swedish woods in which he mentions the method for investigating quantitatively the microarthropods in the soil: desiccating small samples issuing from separate layers by at most slight heating. In 1932 TRÄGÅRDH and FORSSLUND published investigations into the desiccation methods applied in quantitative studies of the soil fauna. In this paper it is clearly shown that desiccating samples of litter by heating yield smaller catches than desiccating samples at the temperature of the room, and that too strong heating is often the main cause of the relatively low numbers of microarthropods in the investigations made up to that moment. The exactness of the results of the method recommended is not stated. In a recent publication (1948) FORSSLUND proved that even in the case of a very slow desiccation of samples of 100 cm³ and 24 cm³ a great part, especially of the thin-skinned microarthropods, get lost.

BORNEBUSCH (1930) made a thorough investigation into the soil fauna of Danish hardwood and softwood forests. From ten different forests: oak-, beech- and spruce-woods, with different forms of decomposition of the litter, during a year 9 samples of 0.1 m² separated in two or three layers were sieved with the aid of a Tullgren-apparatus. The larger animals were identified to species or families and counted. Of mites, collembolae and enchytraeids only the total number was mentioned. Though the numbers of the latter groups are, no doubt, too small because of the temperature applied in desiccating, the size of the samples and the low magnification used in counting the catches, (see

TRÄGÅRDH and FORSSLUND 1932) the essentially different composition of the fauna in mull-soil and that in mor-soil clearly appears from his results. In mull-soils the fauna is to be characterized as a fauna of earthworms in which especially the larger species predominate; in mor-soils the fauna is almost wholly restricted to the organic layers and is for the greater part composed of mites, collembolus, larvae of Diptera and wireworms. The average numbers of the different groups, their weights, and their respiration per hour per m^2 were mutually compared. To the results concerning the rôle of the soil fauna in the decomposition of the litter we will return in chapter VI.

In 1933 ULRICH devoted a quantitative investigation to the macrofauna respectively in the litter of a spruce wood with slow decomposition and in the litter of a mixed beech-oak forest with a fairly good decomposition. During a year monthly samples of 1 l were taken consisting of litter and humus and sieved in a Tullgren-apparatus. The contents of these samples are too big to be justified in expecting reliable values concerning the density of the microarthropods. The samples were considered to be representative for the litter fauna of the whole forest. They were taken from different parts of the forest every date of sampling. The fluctuation in numbers of the whole fauna during the year was found somehow in accordance with the data of the climate. Whether this conformity proves a causal connection may be doubted, however. In the first place it is very unlikely (and it is not proved either) that any sample of 1 l would give a correct idea of the litter fauna in a forest with a surface of 3 ha (spruce) in one case and a surface of 0.5 ha (oak-beech) in the other. Moreover, the proportion of the litter and humus always differs because of the sampling technique. Finally, in order to trace a correlation between climatological circumstances and animal fluctuations, a comparison of the total number of animals or of great groups such as insects and spiders on different points of the year is of no value, since it is not true that all species respond in the same way to changing climatological circumstances during the year. Only for each species separately it would be possible to establish a correlation between fluctuation and precipitation or temperature. Because of the fact that the identification has been made to small systematic groups (mites and collembolus for the greater part into families) this investigation presents, however, valuable material for comparison. To the calculations and the experiments concerning the decomposition we will return in chapter VI.

VON BUTOVITCH and LEHNER (1933) did research work in the field on the macrofauna of an extensive forest area in Brandenburg (Germany). They abandoned the minute desiccation technique and used a mechanic sieve technique. Of 180 samples (0.5×0.5 m) taken between the middle of October and the middle of November the organic layer (A_0) and the mineral one to a depth of 15 cm (A_1 and A_2) were examined. These samples originated from 6 different types of forests. The number of samples varied

from 5 to 36 per type. From the check list of the species it is obvious that some insight is gained only into the biggest species occurring in the greatest density (wireworms, *Brachyderes incanus* L. etc.) Of groundbeetles, rovebeetles, and spiders only some specimens in total were caught. This method does not give an insight into the composition of the community.

VOLZ (1934) investigated the fauna in the different layers of some mull- and mor-soils in Germany. His samples ($10 \times 10 \times 2$ cm) were taken at rather short distances, at least in the mull-soil. They were collected from December up to July with irregular intervals and dried up in a Tullgren-apparatus. Only the Collembola are discussed in detail, Acari, Protura, and Thecamoeba are taken as groups. He concluded to a specific dispersal in the different layers and distinguished: inhabitants of the upper loose litter, inhabitants of the upper soil layer (A_1) and the rawhumus layer and inhabitants of the lower soil layers. Thecamoeba counted in samples of 0.1 cm^3 appeared to be present in very great numbers, especially in the upper layers of the mull-soil.

FOURMAN (1936, 1938, 1939) started his investigations into the significance of the soil fauna for the decomposition of the litter from direct observations in the field with the aid of pocket lenses, binoculars and a pocket microscope. He describes the humification process of tree-stumps in a favourable site and emphasizes the significance of the stumps as hiding and gathering points in winter and especially as centres from which populating the layers of litter might take place. In natural circumstances, the microarthropod population of these stumps may always been immigrated from the adjacent layers of litter and the "Kolonisation der Fläche", if occurring, would be a consequence of more favourable ecological circumstances in the stump, which cause here a strong increase. FOURMAN also thinks an artificial enrichment of the soil fauna possible by carrying a "mixed population" on a tree stump specially prepared for the purpose. In 2 years the population would have extended into a litter layer of 11 cm depth and to a distance of 2 m.

WILLIAMS (1941) made an investigation into the fauna of the soil in a primeval forest without undergrowth in Panama. The larger animals were sought with the naked eye, the smaller ones were collected in a Berlese-apparatus¹). The investigation has mainly systematic value: numerous new species and genera and even a new family were described. The ecological characteristics (occurrence, density) of more or less extensive groups are presented.

In New York EATON and CHANDLER (1942) made an investigation into the composition of the soil fauna in different soil types which were partially investigated in different horizons. The samples measuring $\pm 470 \text{ cm}^3$ were sieved in a Tullgren-apparatus. Earthworms were collected from surfaces of 1 sq. foot wetted with a solution of HgCl_2 , which compelled a great part of the

¹) For description of the Berlese-apparatus see chapter III.

earthworms to come to the surface. To obtain the remaining part, digging out the sample was, however, necessary. Here too, forests with a mull-profile appeared to be rich in earthworms (the species *Lumbricus terrestris* L. and *Allolobophora caliginosa* Sav., both imported from Europe) and relatively deficient in microarthropods, whereas the forests with a mor-profile and the transitional types possessed a great quantity of mites and collemboles but few or no earthworms.

The last two investigations, just as those of HOPE (1943) and PEARSE (1946), show that in America too, the fauna of the soil as to its quantitative composition in larger taxonomic units greatly resembles the N.W.- and middle-European. Here too Acari and Collembola are the most numerous inhabitants, while also the density of earthworms and arthropods depends in the same way on the structure of the soil profile.

In 1943 FORSSLUND published an extensive study of the fauna in the North-Swedish forest soil. In 11 different forests for the greater part consisting of Scotch pines and spruces with different types of undergrowth a total of 38 series of samples and a number of special samples were examined. Each series usually consisted of one sample from the upper layer of litter, one from the layer of litter in decomposition, and one from the humus layer. The samples varied in size from 100—400 cm³. The numbers of animals, all identified to species except in the case of Trombidiformes and Acaridae, are dealt with per dm³. The distribution of the species over the area investigated (frequency s.s. KROGERUS) is given in a frequency curve showing that 51 out of the 140 species occur in 9 or more of the 11 forests, 21 species only occur in one forest. The abundance is expressed in thousands per dm³ and classified into five groups on account of the values found for the Oribatei species. The dominance or relative abundance is expressed in percents of the total number of animals. These values were calculated both for the groups of the Gamasiformes, Trombidiformes, Sarcoptiformes and Collembola, and for the dominating species of the Gamasiformes, Oribatei and Collembola.

For the macrofauna 2 or 3 surfaces of $\frac{1}{16}$ — $\frac{1}{4}$ m² per stand were sieved by means of an insect sieve and the numbers were calculated per m². It was evident that in preserving the samples for a fairly long time (some weeks) a great part of the animals died and chiefly the predatory species survived. It appears from the small numbers of most species that this method is inadequate for a quantitative investigation of the larger species.

As a first complete quantitative analysis of the fauna of microarthropods in different forest types this investigation is of the greatest importance. The origin of the samples of different forests, their small number, and the short period of investigation (June to September) make it impossible to decide to a periodicity of the different species. The conclusion that a periodicity would be absent during this period seems unjustified for the reasons mentioned. FORSSLUND also concludes to a small density of microarthropods in

soil types with a favourable decomposition. The macrofauna, however, is much more developed here.

STRICKLAND (1945, 1947) published two investigations into the fauna of the soil in cocoa-plantations compared with resp. that of native woods and that of a savannah-biotope. For the first investigation he used a method developed in England for investigating the soil fauna of meadows and arable land. This so-called floatation process is based on separating organic and inorganic material by their difference in specific weight and separating the fauna from the organic material by mixing a liquid (petrol, xylol, benzine) that dissolves the wax-layer of the skin, and carries the animals with it in decanting. Though, according to STRICKLAND in this way 95% of the fauna is caught, as appears from examination of the material treated, it seems very improbable to me that the suspended parts of the liquid will sufficiently penetrate to wet all materials in the humus samples, as these wholly consist of organic material in which especially the smaller animals are quite hidden. The small numbers of mites and collemboles caught support this view. For a comparison of the soil fauna of the two biotopes (both litter-covered) this needs not to be an objection. The native woods' fauna appeared to be richer than the soil fauna of the cocoa-plantations.

In the second investigation a Berlese-apparatus was used. In the two biotopes a downward migration of mites and collemboles could be stated with decreasing humidity. The fauna of the cocoa-plantation was richer than that of the savannah.

ELSE JAHN (1944) made an investigation into the fauna of the soil in pine afforestations of different ages in an area of drift-sands in Austria. In forests of *Pinus nigra* resp. 14, 46, and 92 years old — the second of which was mixed with oaks — from May 1942 to April 1943 monthly samples of 1 l from the litter layer and the soil were examined with the aid of a Berlese-apparatus. From the fluctuation in the total numbers of all animals conclusions are drawn concerning the influence of the climate on the development and the vertical movement of the whole fauna in the different types of forest. It is evident from her investigation that the fauna of the soil increases quantitatively with increasing age and thickness of the layer of litter. This is chiefly caused by the fauna of mites. The collemboles only increase to a small degree, *Scutigerella immaculata* and *Troctes silvarum* even decrease in density.

From the above survey it appears that the quantitative investigation into the fauna of the forest soil has always been performed on samples that were examined in a direct or an indirect way.

The direct way of examination always appears entirely insufficient for the smaller inhabitants of the soil. For the larger animals of the soil reliable values are only found when a long time is spent on the investigation. The indirect method was in practice always performed with the aid of the desiccation method of Berlese-

Tullgren. With this method animals of a quite different order of size were examined quantitatively in the same samples. For the macrofauna these samples were often too small to be representative; for microarthropods the same samples were too large to get reliable data with the desiccation technique. Even students who worked with samples of different sizes did not at all or only insufficiently check the reliability of their catching technique. For this reason the investigations mentioned are not at all or only with reserve to be compared mutually in a quantitative respect.

No doubt, the very laborious examination technique is the cause that in none of the investigations the samples were examined in a large number of parallels. Generally single samples are considered sufficient to characterize the fauna of the soil in a certain forest and at a certain time. That in this way the horizontal variation in the composition of the soil fauna is wholly left out of consideration, does not, or only to a small extent, make the results mutually comparable. Further objections to several investigations are: the insufficient homogeneity as regards the composition of the samples compared, and the mutual comparison of the total number of animals met with in the samples. As we shall see, the density of most species in layers of litter with a different degree of decomposition is quite different so that samples that will be compared mutually, should consist of material as homogeneous as possible. The comparison of total numbers of animals has little value especially if in these numbers animals of divergent sizes are represented such as mites and beetles. The much larger numbers of the smaller animals will completely eclipse those of the larger animals and in this way only give a deformed view of the density of the fauna of microarthropods. Also the interpretation of the fluctuation of the total numbers of animals in terms of climatological phenomena makes little sense: the fauna is composed of species each having their own rhythm of development and responding to environmental circumstances in their own way. The effect as it is reflected in the fluctuation of the total numbers does not give an insight into the phenomena that have taken place in reality.

In qualitative respect these investigations teach us that the soil fauna in forests of different zones is in the main composed of the same larger taxonomic units: all phyla adapted to terrestrial life have their representatives in the forest soil. Though mites and collembolids always have the highest numbers it is not yet certain, because of their small size, that these groups take the most important place as to the total body weights and volumes. It is evident, however, that these groups occur in a considerably lower density per volume-unit of litter in forests with a thin layer (young forests and forests with a quick decomposition of the litter) than in woods with a thick litter layer. Of several forms of the macrofauna (earthworms, millipedes, larvae of tipulids) the density appears to be larger in the case of a quicker decomposition of the litter and a better structure of the soil.

In this summary only the most important investigations into the domain of the analysis of the fauna of forest soil were mentioned. Many investigations had to remain undiscussed. In the bibliography, however, they are mentioned more completely. For a recent and very extensive bibliography see KÜHNELT (1950).

The purpose of the present investigation is to give a detailed description of the animal community in a forest soil including its vertical dispersion in the different layers, its horizontal dispersal in the area investigated and its fluctuations during the course of the year. For this purpose a great number of samples of different sizes was examined throughout the year and a method for the investigation of the soil surface fauna (epedaphic macrofauna) was developed. In all cases it was intended to take as many samples as was possible. The investigation was restricted to one area: a beech forest without any undergrowth and with a well developed litter and humus layer. The reasons why this particular stand was chosen were stressed already in the introduction (p. 4).

Not all animals caught in this investigation were identified to species¹⁾. In general those species, which occurred in small density and frequency were taken together into larger taxonomic groups. Unfortunately, this had also to be done with groups, which offered great difficulties in identifying. I am aware of the imperfection of the description of the animal community by this. Notwithstanding this incompleteness I think the results give a fairly good impression of the complicated structure of the animal community of forest soil.

CHAPTER III

METHODS FOR THE QUANTITATIVE RESEARCH INTO THE FAUNA OF THE SOIL

A. DIRECT METHODS OF INVESTIGATION

For the quantitative investigation of the fauna of the soil different methods can be applied. The most obvious manner of investigation is the direct observation of bigger species with the naked eye, of smaller ones with the aid of a loupe, or a binocular microscope. The direct examination of the litter layer for the larger animals can be made more easily by using a shaking sieve. By shaking the material it is divided into two, if necessary into more parts, which can be better investigated separately than the original material. The measure of the surface to be investigated is limited by the practicability of the investigation. If it is the intention to gather quantitatively the whole fauna visible to the naked eye a surface of 50×50 cm is the largest possible. To examine this surface carefully required several hours hard work. In a longer course

¹⁾ With regard to those animals identified to species and discussed in the special parts of the sections V A, C and D the abbreviations of the author names in the scientific names are only mentioned in these parts.

Table 1. The composition of the soil fauna in 10 samples each of $\frac{1}{4}$ m² in a young oak forest. Samples taken from 25 VI to 17 VIII 1945¹⁾.

Number of the sample :	1	2	3	4	5	6	7	8	9	10
<i>Lumbricus rubellus</i>	7	7	3	1	15	1	1	—	1	—
<i>Arion subfuscus</i>	—	1	—	—	—	—	—	—	—	—
Geophilidae	1	4	—	—	2	—	1	11	—	1
<i>Lithobius forficatus</i>	—	2	2	2	5	1	—	—	1	—
<i>Lithobius calcaratus</i>	11	5	3	6	11	2	4	1	4	2
<i>Cylindrojulus silvarum</i>	2	2	4	2	24	1	—	10	8	1
<i>Ectobius silvestris</i>	1	4	2	1	—	1	2	—	—	—
<i>Calathus micropterus</i>	—	—	—	1	1	—	—	—	—	—
<i>Pterostichus oblongopunctatus</i>	1	—	—	—	—	—	—	—	—	—
<i>Abax parallelus</i>	1	—	—	—	—	—	—	1	—	—
<i>Staphylinus chalconcephalus</i>	—	—	4	—	—	—	—	—	—	—
<i>Staphylinus</i> sp. 1.	—	—	—	—	2	—	2	—	—	—
Staphylinidae several species	4	5	2	—	9	2	1	3	1	—
<i>Xylodrepa quadripunctata</i>	—	—	—	—	—	—	—	1	—	—
<i>Phosphuga atrata</i> l.	—	—	1	—	—	—	—	—	—	—
<i>Geotrupes silvaticus</i>	—	2	—	—	—	—	—	—	—	—
<i>Serica brunnea</i>	—	2	2	—	—	—	—	—	—	—
<i>Athous subfuscus</i> l.	4	1	—	—	3	—	—	2	—	—
<i>Dolopius marginatus</i> l.	3	3	—	1	7	—	—	—	1	—
<i>Ectinus aterrimus</i> l.	3	4	1	1	3	1	1	2	1	—
<i>Sericus brunneus</i> l.	—	—	—	—	—	—	2	—	—	—
<i>Helops laevioctostriatus</i> l.	—	—	—	—	2	—	1	1	1	2
<i>Strophosomus melanogrammus</i>	—	—	—	2	1	—	—	—	—	—
<i>Strophosomus</i> sp. 1. and p.	3	4	3	4	5	—	1	5	—	—
<i>Tipula</i> sp. 1. and p.	1	4	2	1	1	1	—	—	—	1
<i>Agrotis</i> sp. 1. and p.	1	—	1	—	—	—	—	3	1	—
<i>Stenamma Westwoodi</i>	—	1n	—	—	—	—	—	—	1n	—
<i>Myrmica ruginodis</i>	+	+	—	+	—	—	—	—	1n	1n
<i>Lasius niger</i>	—	—	—	—	—	—	—	1	—	—
<i>Formica fusca</i>	—	+	—	—	1n	—	—	—	+	1n
Araneina	4	10	24	6	2	10	6	—	10	1
Opiliones	—	—	7	1	—	—	—	—	—	—

n = nest + = number of animals not counted

of time attention will relax in consequence of which an uncontrollable source of mistakes will arise.

It is of importance to know how far this direct method gives a representative impression of the composition of the animal community as to its larger elements.

Two questions are of importance: the occurrence of the species in the samples (frequency) and the number of the individuals (density). In table 1 a survey is given of 10 samples of 50×50 cm in a young forest of oaks. This shows that in using this method of examination only a few species are found in a high frequency (*Lumbricus rubellus*, *Lithobius calcaratus*, *Cylindrojulus silvarum* and *Ectinus aterrimus*). Whether the numbers of the individuals of these species give a real impression of their density has to be examined. However, their density and dispersion is such that they appear in at least 8 from 10 samples.

¹⁾ In this and following tables insect larvae and pupae are indicated by l. and p. respectively. No indication at insect groups or species means imagines.

Where the frequency percentage ($F\%$) is low, this may be attributed to the incapacity of the method through which far fewer animals are caught than there are in reality. But the low $F\%$ may also be a consequence of the small density or of the heterogeneous dispersion of the species. Without further research into the reliability of the method it is not possible to state the real cause of the low frequency.

In order to test the reliability of direct examination of samples in the field a surface of $\frac{1}{4} \text{ m}^2$ of litter of beeches separated into upper, middle and lower layers of litter (resp. F_0 , F_1 , F_x), was examined on the spot with the aid of a shaking sieve under rather unfavourable circumstances: chilly dark weather. The investigated material was transported to the laboratory in canvas bags where it was transferred to Tullgren-apparatuses¹⁾. Samples from the humuslayer (H) and the upper 3 cm of the mineral substrate (A_1) were examined at the laboratory under the most favourable circumstances of light and temperature and afterwards sieved in Tullgren-apparatuses. Table 2 gives the species with their numbers and lengths in mm which were caught in the different layers resp. in the field (in the laboratory) and in the Tullgren-apparatus. This table shows that only a very small part of the fauna which should be caught in the direct way in consequence of its size, is caught in reality. No doubt the unfavourable circumstances and the great dampness of the substrate caused even big animals (earthworms of a length of 35 mm!) to remain unobserved. On the other hand it was evident that many and even big animals also stayed behind in the material examined in the laboratory. These numbers are so large that the numbers found at direct examination are of little or no value for estimating the real density. To compare samples in different types of wood (VON BUTOVITCH and LEHNER 1933) the reliability of the results will be influenced moreover by the structure of the layer of litter and humus, which varies in the different types of wood. This direct method of observation may be considered unsuitable for obtaining reliable quantitative data. So neither the frequencies nor the numbers of individuals in the examination mentioned above (table 1) are right.

In order to get a first orientation concerning the qualitative composition of the macrofauna, this method which needs not to be limited to $\frac{1}{4} \text{ m}^2$ of course, retains its value.

A direct method, which is often used in determining the relative density is the method of DAHL (1921), who took the animals caught in a fixed time as a measure of their density. HEROLD (1929) applied this method to Isopoda, RENKONEN (1938) to terrestrial beetles. Often, however, meteorological circumstances, seasonal fluctuations in appearance or in the activity of the animals, and the different structure of the biotopes to be compared may be factors that make comparison of the results impossible. An insight

¹⁾ For a description of this apparatus see p. 31.

Table 2. Check on direct investigation method.

Examination of the litter with shaking sieve (in the field)	Material examined, sieved in Tullgren-apparatus	
	Material which passed through the shaking sieve	Residue on the shaking sieve
F ₀ 4 <i>Arion subfuscus</i> (8) 4 <i>Araneina</i> (3-4) 1 <i>Entomobryidae</i> (4)		1 <i>Dendrobaena</i> sp. (30) 1 <i>Enchytraeidae</i> (10) 1 <i>Diptera</i> l. (5)
F ₁ 2 <i>Enchytraeidae</i> (10) 1 <i>Julus</i> sp. (15) 2 <i>Entomobryidae</i> (3, 5) 2 <i>Staphylinidae</i> (3, 4) 1 <i>Staphylinidae</i> l. (2) 1 <i>Anthomyidae</i> l. (4) 1 <i>Dolichopodidae</i> l. (3) 1 <i>Obisium muscorum</i> (3) 4 <i>Araneina</i> (2-4) 1 <i>Drassidae</i> (8)	5 <i>Entomobryidae</i> (2-4) 1 <i>Acrotrichis</i> sp. (2) 1 <i>Staphylinidae</i> (4) 2 <i>Staphylinidae</i> l. (5, 6) 2 <i>Cantharidae</i> l. (3, 7) 20 <i>Anthomyidae</i> l. (4, 5) 3 <i>Dolichopodidae</i> l. (4) 1 <i>Obisium muscorum</i> (3) 2 <i>Araneina</i> (2) 1 <i>Nemastoma lugubre</i> (3)	4 <i>Dendrobaena</i> sp. (15, 35) 15 <i>Enchytraeidae</i> (5-10) 1 <i>Arion subfuscus</i> (25) 1 <i>Pentatomidae</i> (8) 4 <i>Cantharidae</i> l. (3-4) 25 <i>Anthomyidae</i> l. (4-5)
F _x 1 <i>Dendrobaena</i> sp. (20) 1 <i>Julus</i> sp. (5) 1 <i>Entomobryidae</i> (4) 9 <i>Staphylinidae</i> (3-7) 1 <i>Cantharidae</i> l. (7) 1 <i>Athous subfuscus</i> l. (10) 1 <i>Anatis ocellata</i> 1 <i>Coccinella bipunctata</i> 1 <i>Anthomyidae</i> l. (4) 10 <i>Araneina</i> (2-4) 1 <i>Araneina</i> (8)	6 <i>Dendrobaena</i> sp. (10-35) 9 <i>Enchytraeidae</i> (10) 1 <i>Arion subfuscus</i> (3) 4 <i>Julus</i> sp. (4-5) 1 <i>Acrotrichis</i> sp. (2) 16 <i>Staphylinidae</i> (4-7) 4 <i>Staphylinidae</i> l. (3-5) 20 <i>Cantharidae</i> l. (4-7) 2 <i>Athous subfuscus</i> l. (4, 9) 2 <i>Incurvariidae</i> l. (5) 9 <i>Anthomyidae</i> l. (4-5) 10 <i>Dolichopodidae</i> l. (3) 2 <i>Obisium muscorum</i> (3) 4 <i>Araneina</i> (2-3)	2 <i>Dendrobaena</i> sp. (15, 7) 3 <i>Enchytraeidae</i> (10) 2 <i>Julus</i> sp. (5) 1 <i>Acrotrichis</i> sp. (2) 3 <i>Staphylinidae</i> (3-5) 2 <i>Staphylinidae</i> l. (3-5) 7 <i>Cantharidae</i> l. (4-7) 1 <i>Strophosomus</i> sp. l. (3) 3 <i>Anthomyidae</i> l. (4) 10 <i>Diptera</i> l. (3) 1 <i>Araneina</i> (3)

Examination of the humus and mineral substance by sorting out the sample in the laboratory	Material examined sieved in Tullgren-apparatus	
H 3 <i>Dendrobaena</i> sp. (15-25) 2 <i>Geophilidae</i> (15, 20) 6 <i>Julus</i> sp. (4-20) 1 <i>Pentatomidae</i> (8) 6 <i>Staphylinidae</i> (3-5) 2 <i>Staphylinidae</i> l. (5, 9) 10 <i>Cantharidae</i> l. (5-10) 4 <i>Athous subfuscus</i> l. (9-11) 1 <i>Curculionidae</i> l. (8) 2 <i>Dolichopodidae</i> l. (5, 7) 5 <i>Diptera</i> l. (3-6)	1 <i>Enchytraeidae</i> (10) 7 <i>Julus</i> sp. (5-10) 14 <i>Staphylinidae</i> (4-7) 17 <i>Staphylinidae</i> l. (5-9) 24 <i>Cantharidae</i> l. (4-10) 1 <i>Dolopius marginatus</i> l. (7) 15 <i>Athous subfuscus</i> l. (3-10) 1 <i>Incurvariidae</i> l. (5) 2 <i>Rhagio lineola</i> l. (9) 11 <i>Mycetophilidae</i> l. (7) 18 <i>Diptera</i> l. (4-6) 2 <i>Araneina</i> (2-3) 2 <i>Julus</i> sp. (5)	
A ₁ 1 <i>Lithobius calcaratus</i> (20) 3 <i>Julus</i> sp. (10-15) 3 <i>Staphylinidae</i> (3-7) 9 <i>Cantharidae</i> l. (5-8) 1 <i>Carabidae</i> l. (7) 4 <i>Athous subfuscus</i> l. (6-10) 2 <i>Dolopius marginatus</i> (8-10) 4 <i>Diptera</i> l. (3-5) 5 <i>Dendrobaena</i> sp. (20-35)	1 <i>Staphylinidae</i> (4) 5 <i>Staphylinidae</i> l. (3-5) 10 <i>Cantharidae</i> l. (4-7) 1 <i>Helops laevisoctostriatus</i> l. (12) 10 <i>Athous subfuscus</i> l. (5-10) 3 <i>Dolopius marginatus</i> l. (6-8) 2 <i>Rhagio lineola</i> l. (6) 2 <i>Mycetophilidae</i> l. (6) 20 <i>Diptera</i> l. (3-6)	

into the absolute density of the species this method does not give us at all.

For examination of animals not visible to the unaided eye FRANZ (1942) applied a direct method in investigating the presence of nematodes in the soil of meadows and fields. Small quantities ($\frac{1}{2}$ —1 gr) of crumbled substrate are examined under a dissecting microscope with a magnifying power of 80 times. This method appears to be the best for quantitative work in this group. Examination of samples of litter, however, gives the same trouble as macroscopical examination: because of the kind of the material numerous animals will not be observed.

Several groups of animals, however, cannot be quantitatively determined except by direct observation, such as ants, snails and animals that are in the forest floor in cocoon or nymph stage. Further those species must be counted among this group which appear in too small a density to be able to gather them from the samples of soil in an indirect way and cannot be determined quantitatively in another way either (e.g. by means of the trap technique). In general these species, however, will have a subordinate place in the community by the very fact of their small density which makes the absence of reliable determination of their density not so serious.

For ants QUISPEL (1941) worked out a method which is applied by WESTHOFF and WESTHOFF-DE JONCHEERE (1942) on a large scale and to the reliability of which they concluded. He determined the number of nests of the different species on a sufficiently large surface — generally 100 m² — by rooting up the whole layer of litter and the upmost mineral layer with the aid of a little rake and by examining it. As whole nests were counted, the difficulty of nests remaining unobserved was not great.

In general snails are not driven out from the substrate by desiccating, but withdraw into their shells. In quantitative investigations their number has to be fixed by picking off a certain surface just as in the case of cocoons of insects, which of course cannot be caught by desiccation either. At the quantitative investigations of this group a rather large margin of mistakes ought to be taken into consideration, which is in a high degree dependent on the time that can be spent on the examination of the surface and the experience of the student. At a research into the reliability of countings of cocoons of *Bupalus piniarius* L. in 1 m² of forest soil by trained men HOUTERMANS (1939) found, that on an average 78% of the cocoons were found. No doubt prolongation of the time of the research might have raised this percentage for cocoons of this measure.

A quantitative investigation of the fauna of snails by a direct method was executed by ÖKLAND (1929, 1930) and in our country by MÖRZER BRUYN (1947). Their very accurate method of investigation of small surfaces resp. $\frac{1}{8}$ and $\frac{1}{4}$ m² gives a high reliability to their results. Comparison of non-simultaneous investigations as replicates, however, remains dangerous as can be

concluded from the fact that ÖKLAND, repeating an investigation in a certain place after a year, found that species of low abundance had been substituted by others, and species of high abundance had grown less abundant.

The great difference between the number of animals observed directly and the number of animals minimally present in a forest soil sample (table 2) shows that a repetition of the investigation would not give sufficient indication of the number really present, as was the case at the investigation of the density of birds of PALMGREN (1930). The latter found in an experimental way that the number of birds observed should be raised by 60% after one investigation, by 25% after two, by 10% after three and by 4% after four investigations. KROGERUS (1932) who performed an investigation of the fauna of the arthropods along the Finnish coast, thinks that in examining small surfaces (1 m²) there is a greater possibility of obtaining exact numbers and it is not necessary to correct the numbers found. This may be right for the area investigated by KROGERUS, which was not of a complicated structure; in the case of examination of the forest soil this argument does not hold. Anyhow, at a quantitative investigation of the layers of litter a correction as PALMGREN used, which ought to be different for each species and each type of litter moreover, has no sense.

B. INDIRECT METHODS OF INVESTIGATION

1. Introduction

From what has been said it follows that in general the direct way of investigating must be abandoned in case of a quantitative investigation of the fauna of the soil. There are several indirect methods for studying the composition of the fauna of the soil in quantitative respect. These methods which all spring from separating fauna and substrate can be brought under the following heads:

a. Sieving the sample either with or without the use of water (MORRIS 1922, LANE and SHIRCK 1928). In a semi-dry condition the soil is shaken through sieves with meshes of different widths or washed by means of a jet of water through successive sieves. The animals staying behind, which, however, are often damaged, can then be picked up from the residue.

b. Separating the fauna from the substrate by the difference of their specific weight. By itself this method is only efficient when the substrate contains no or few coarser fragments of plants. THOMPSON (1924), EDWARDS (1929) and DANIELS (1933) preceded the "floatation technique" by sieving through meshes of different widths. LADELL (1936) used a solution of MgSO₄ with a specific weight of 1.11, which peptized the material. In order to facilitate the separation of the fauna and the substrate a strong stream of small air bubbles was carried through the sample suspension. Even eggs of collembolus could be separated quantitatively in this way.

If in the material floating on the surface the quantity of vege-

table material is high, then the fauna of arthropods can be separated from this material by the following method. After cooking the suspension in order to remove the air a layer of benzol (GALT and HOLICK 1944) or paraffin (COOCKBILL et al. 1945) is added. By solution of the layer of wax on the skin of chitin, the arthropods are surrounded by the paraffin and can be decanted with it. In this way about 98% of the wireworms are supposed to be caught.

c. Desiccating the sample slowly on a sieve. A great part of the animals escapes the substrate through the sieve, and is caught via a funnel in a gathering glass with a killing and conserving liquid. BERLESE (1905) effected desiccation by surrounding the funnel, in which the sieve with the sample was placed, with a warm water mantle. TULLGREN (1917) and after him many others used for the same purpose an electric bulb suspended above the material in the sieve.

d. Mechanical, chemical or electrical irritation of the soil animals. This irritation often causes a flight reaction of the soil inhabitants especially of earthworms by which part of them appear at the soil surface. Mechanical irritation is effected by shaking a spade in the soil, a well-known catching method for earthworms. Several chemical irritants are used for driving out earthworms. EVANS and McL. GUILD (1947) used potassiumpermanganate dissolved in water in their field studies on earthworms. EATON and CHANDLER (1942) applied a dissolution of HgCl_2 on a surface of forest soil, surrounded by an iron frame. In both cases digging out the soil afterwards, however, produced still more animals. Electric currents are used by DOEKSEN (1950), the results of which are not to express on a certain surface unit in the present stage of development.

e. Immersing the samples enveloped in a piece of canvas into a funnel filled with water. Nematodes, enchytraeids, rotifers and tardigrads free themselves from the substrate for the greater part, fall into the funnel and can be gathered by opening a tap (BAERMANN 1917).

f. Simltaneous catching of autochthonous animals and animals that in known numbers have been marked and been released. From the number of autochthonous animals caught and the ratio between the number of animals recaught and the number of animals released (Lincoln-index) the total density of the population can be calculated (LINCOLN 1930, JACKSON 1939, DOWDESWELL et al. 1940).

The methods mentioned sub. a and b were not used for this investigation. As was already said the structure of layers of litter and humus is very compact. Moulds often unite the elements of litter into parts difficult to divide, roots of tree branch out very much in the layer of litter and keep the humus parts tightly together. Owing to this the material is neither suitable for sieving nor for floatation. In the latter case almost 100% of the material would float on the surface after a floatation with brine.

The mineral substrate might be examined by using one of these methods. In the forest soil concerned in this investigation it contains only a fraction of the fauna of the layers above, so it was always examined in the same way as the layers of humus and litter.

BERLESE's desiccation technique, modified by TULLGREN appears to be the most suitable for a quantitative investigation of micro- and macroarthropods, the latter as far as they occur in a sufficient density. To small worms, enchytraeids, nematodes, tardigrads and rotatoria another method must be applied. Either these animals desiccate and die or they pass into an anabiotic form. Fairly good results were obtained by the method of immersing the sample into water. Only a small number of samples was investigated thus by way of orientation. The technique of these two methods will be discussed in the sections 3 and 4 of this chapter. As these two methods will be practised on samples, the way of taking samples will first be explained (section 2).

The complicated structure of the organic layer prevented application of the methods mentioned under d. Earthworms were also caught in desiccating samples of 4 dm³.

The last method mentioned above (f) is applied on some macroarthropods with a small density, but very active at the surface of the soil (several beetle and spider species). It will be discussed in section 5 of this chapter.

2. Method of Sampling

In investigating the fauna of the forest soil in detail the obvious method is to examine the fauna of the morphologically distinguishable layers in the litter profile separately. Especially with small animals this differentiation is valuable as these animals can be expected to live in a small habitat. The different layers of litter to distinguish will be mentioned in the next chapter. As to the macrofauna a less detailed differentiation will do.

Originally the samples taken for small animals (e.g. mites and collembolus) and bigger animals (many insects and their larvae) measured resp. 1 dm² and 0.1 m² with a height of 1-3 cm, dependent on the thickness of the layer. In practice it turned out that the former were too large, the latter too small. In desiccating the samples of 1 dm² so many mites and collembolus were caught and so much undesirable organic material fell through the sieve that the catch could not be counted exactly. On the other hand too small a number of bigger animals was caught in desiccating samples of 0.1 m². The incomparability of samples of the same surface, however, proved to be another difficulty. Even in woods with an apparently regularly developed layer of litter the thickness of the separable layers proved to vary much at a closer examination. For this reason parallel samples of the same layer taken at a short distance from each other, may show differences in weight from 200-500%. This difficulty is the greater in comparing samples that have been taken from layers of litter situated under one

another. It is clear that the same thickness cannot be expected here. To avoid these difficulties the method of taking samples of a certain surface was abandoned, and the volume was taken to characterize the size of the sample. Besides the fact that all samples of equal volume are comparable mutually on this base, it must be voted that the litter and soil fauna do not live on the soil surface but *in* the litter or soil substrate. So the volume is a better characteristic for soil samples than the surface.

To ascertain the sizes of the samples it is necessary to consider the sizes of the different soil animals.

The greatly varying sizes of the different soil animals require a distinction of the forest soil fauna into several groups. The names and limits of these groups chosen by me, are presented in fig. 1. Each group takes a similar distance on a logarithmic scale of the

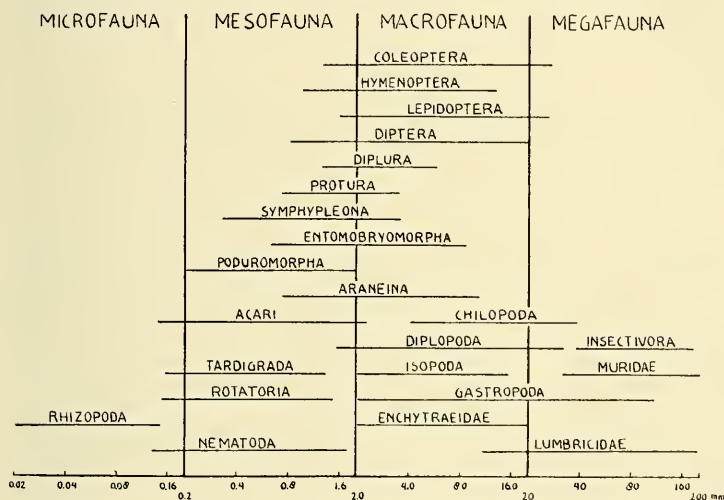


Fig. 1. Division of the soil fauna with regard to the individual length in the principal groups.

range of sizes. The "microfauna" ranging from 0.02-0.2 mm only comprises the Rhizopoda. To the group of the "mesofauna" (0.2-2 mm) belong the microarthropods (Acari and part of the Collembola: Poduromorpha, Entomobryomorpha and Symphypleona), Nematoda, Tardigrada and Rotatoria. The group of the "macrofauna" (2-20 mm) includes the Enchytraeidae, the greater part of the Mollusca, Myriapoda and Araneina and most orders of the Insecta. At last the "megafauna" (2-20 cm) comprises Lumbricidae and Vertebrata.

Of course this division has all the drawbacks of an artificial grouping. Several groups of animals are just between two groups e.g. Tardigrada and Rotatoria (micro-mesofauna), several families

of Collembola and Protura (meso-macrofauna) and a number of Mollusca and Myriapoda (macro-megafauna). Nevertheless this division gives a clear idea of the very great variation in size of the members of the animal community in the forest soil.

Together with this variation in size there is a great variation in density. In a sample of litter of 1 dm³ some Myriapoda, Diplura, larvae of Diptera etc. may be found. The numbers of Acari, Nematoda, Rotatoria etc., which we find when using a right method of collecting, run into thousands. In the same sample the number of Rhizopoda runs into millions (VOLZ 1934).

The volume of the samples is in the first place dependent on the body volume of the group of animals concerned. As the average body sizes of micro-, meso- and macrofauna are in the ratio of 1 : 100, the average body volumes of animals agreeing in shape are in the proportion of 1 : 1000 : 1,000,000. The samples in which these three groups are studied have to be in about the same proportion as the body volumes of the animals concerned. Expressing the volume of the samples for microfauna in mm³, the volume of mesofauna samples must be expressed in cm³ and the volume of samples for macrofauna in dm³. Moreover, the samples have to be of such volume that the species sufficiently find expression and that it is practicable to collect the species concerned quantitatively.

In practice in the case of mesofauna it proved satisfactory to get samples of comparable volume and homogeneous composition by filling a square box with a volume of exactly 40 cm³ with material of a certain layer by the aid of forceps, scissors and knife.

The measured quantity can be taken to the laboratory in the sampling box or in a petri-dish. The samples of 40 cm³ are satisfactory for the quantitative investigation of most species of mesofauna. The number of specimens of the quantitatively important species varies from a few to about a hundred.

In desiccating the samples the quantity of unwanted organic material that falls into the catching vessels generally causes no trouble in recognizing and counting the specimens.

The method of sampling is somewhat rough for an exact fixing of the volume. If in this way the samples were not entirely comparable as to the number of animals they contain, then the numbers of one species in 10 parallel samples would show a greater divergence from their average than the numbers calculated to the average weight of the samples from their average. For two species viz. *Nothrus silvestris* adult and *Oppia neerlandica* this calculation was carried out (table 3). The numbers were not calculated on the average weight of the samples being 4.6 and 4.9 g but on 5.0 g. In both cases the coefficients of the variation of the calculated value appeared to be still somewhat higher than those of the stated values. So the deviations of the volumes are so small that the volume fixed in this way can be used without any objection as the unit for expressing the density of population.

Table 3. Numbers of *Nothrus silvestris* and *Oppia neerlandica* in 10 samples of 40 cm³ from the F_x layer of the beech forest 8 G on 31 I '47 and 7 II '47 respectively.

<i>Nothrus silvestris</i>			<i>Oppia neerlandica</i>		
Air-dry weight of the samples in g	Number of animals per sample	Number of animals per 5 g	Air-dry weight of the samples in g	Number of animals per sample	Number of animals per 5 g
4.4	15	17	4.7	110	117
4.8	15	16	5.3	89	84
4.5	16	18	4.7	118	126
4.2	1	1	4.8	80	83
4.4	2	2	5.8	142	122
5.3	8	8	5.1	116	114
4.3	27	31	4.6	278	302
4.7	21	22	4.6	165	179
4.7	7	7	4.5	112	124
4.5	18	20	4.7	114	121
Average number of animals: per 40 cm ³ (average weight 4.6 g): 13.0 ± 2.64 coeff. of var. 0.64 per 5 g: 14.2 ± 3.02 coeff of var. 0.67			Average number of animals: per 40 cm ³ (average weight 4.88 g): 132.4 ± 17.9 coeff. of var. 0.43 per 5 g: 137.2 ± 20.4 coeff. of var. 0.46		

In comparison with the samples of the mesofauna the samples of the macrofauna would have to be 40 dm³ being 1000 × as big as those for the mesofauna. Such a sample is much too big to be examined. Samples of 4 dm³ were used, which were taken in tight-closing measuring boxes.

In consequence of the practical necessity of reducing the samples of the macrofauna from 40 to 4 dm³, a number of species will not get their due in these samples. Some of these, however, take such an important place in the community that it is of interest to know their density. If the species is easy to catch and mark and has not an active radius too great, the density can be determined by means of the Lincoln-index (section 5).

3. Desiccation Technique

Numerous are the methods applied by entomologists to gather arthropods by slow desiccation of samples of litter. REITTER, GÄNGELBAUER and LEONHARD entice the animals from the drying material to a piece of damp linen. DODERO causes them to fall through a sieve into water. MOCZARSKI desiccates the samples in bags of a coarse material suspended in a funnel of linen, to which a bottle for catching the animals has been fastened. The long course of time necessary to get results from these methods makes them unsuitable for a quantitative investigation, as it is inevitable that part of the animals falls a victim to the predatory enemies present. A quicker method of desiccating samples was described by

BERLESE (1905) and KRAUSSE (1915). They spread the samples on a sieve, which was placed in the top of a metal funnel. By surrounding the funnel (BERLESE) or only the sieve (KRAUSSE) with a tank with hot water (60–100° C) the sample was desiccated in a few hours. All methods mentioned, which were amply discussed by PILLAI (1922), were never intended for quantitative work by the investigators. For this work the most suitable of these methods is the one described by BERLESE, which method is applied by several students of the litter layer.

TULLGREN (1917) modified this method by desiccating the samples by means of one or more electric bulbs suspended about 5 cm above the sample. Not only the desiccation but also the light urges the animals to creep down. According to TULLGREN after two hours all animals have fallen through the sieve and come down via a funnel into a catching vessel, when the layer is 2-3 cm thick and the temperature is 50° C. Though TULLGREN did not intend this method either for quantitative examination, many investigators have used it for this purpose without any alteration.

TRÄGÅRDH and FORSSLUND (1932) made an investigation into the progress of the catches during the process of desiccation. They used bulbs of different strength and so applied different temperatures in desiccating the samples. Material as homogeneous as possible was heated to resp. $\pm 50^{\circ}$ C and 40° C while a third sample was desiccated at the temperature of the room ($\pm 20^{\circ}$ C). Especially Oligochaeta (enchytraeids) and mites with a thin skin of chitin (e.g. Trombidiformes and larvae and nymphae of Oribatei) were caught in considerably smaller numbers at temperatures of 40 and 50° C, than at the temperature of the room. This is to be expected with enchytraeids, as a desiccating technique will never yield reliable values for these delicate animals. Also the number of these animals caught at 20° C will be only part of the number of animals really present. That larvae and nymphae of Oribatei would be less resistant against dryness — as is stated by them — is refuted by HAARLÖV (1947) for *Platynothrus peltifer* (Koch) and *Notaspis coleoptratus* (L.). Our catches of adult and juvenile specimens also refuted this opinion. This lower resistance against dryness may be true of the very delicate Trombidiformes, which no doubt form a great percentage of the "thin-skinned" mites.

Yet the differences in the catches of heated and non-heated samples may not entirely be interpreted as losses in the former. According to our experience even samples of perfectly similar composition treated in the same way may present very considerable differences in the number of animals, so that, in consequence of the applied method, the difference may be greater but also smaller than those stated. The only way of determining the losses in this manner, is to apply the different methods to large series of samples taken at the same time. Then the results can be worked out statistically. This requires, however, such an extensive apparatus and so much time that we must be content with the indication found, that in applying higher temperatures a considerable part of the fauna is not caught.

A question which is very important and to which the experiments mentioned above do not give an answer, is the question which percentage of the animals present is caught even in applying the most suitable method of working. Before we treat this question we will first discuss the process of desiccating.

In desiccating a sample of litter with the method of TULLGREN the upper layer is first heated. In using not too strong a bulb at not too short a distance the whole surface of the sample is rather equally and very moderately heated. During the evaporating of the water in this upper layer the temperature is only raised to about 25° C. The bigger animals have ample opportunity of withdrawing into the lower moist layers. As to the macrofauna enchytraeids and some larvae of flies do not withdraw, they partly desiccate in the litter. The microarthropods, of which especially the Oribatei move very slowly, are also able to remain ahead of the continuing desiccation. To illustrate this, of four samples as homogeneous as possible gathered close to each other, two were sieved spread in a thin layer, the other two sieved in the intact natural condition. In the former case the layer was ± 1 cm thick, in the latter $2\frac{1}{2}$ -3 cm.

Table 4. Catches of microarthropods in samples of beech litter, spread out on the sieve (I and II) and in similar samples left intact III and IV.

	I	II	III	IV
Air-dry weight in g	6.1	4.9	4.7	4.3
Water contents in vol % .	34.8	41.0	36.0	35.3
Thickness of the layer on the sieve in cm.	1	1	$2\frac{1}{2}$	$2\frac{1}{2}$ -3
Catches after	16 hrs	16 hrs	16 + 24 + 24 hrs	16 + 24 + 24 hrs
<i>Hypochthonius rufulus</i> juv.	3	6	0 + 1 + 3 = 4	0 + 1 + 1 = 2
id. ad.	2	4	0 + 3 + 0 = 3	2 + 0 + 0 = 2
<i>Nothrus silvestris</i> juv.	85	100	13 + 23 + 47 = 83	13 + 17 + 43 = 72
id. ad.	17	50	11 + 3 + 17 = 31	12 + 12 + 15 = 39
<i>Oppia neerlandica</i>	30	55	11 + 10 + 45 = 55	10 + 6 + 27 = 43
<i>Anoetus deuto-nymphae</i>	25	7	86 + 41 + 57 = 164	5 + 1 + 2 = 8
Parasitiformes	4	17	5 + 3 + 13 = 21	1 + 7 + 12 = 20
Trombidiformes	25	24	9 + 18 + 31 = 58	10 + 14 + 9 = 33
Poduromorpha	42	30	11 + 9 + 2 = 22	12 + 18 + 3 = 33

Table 4 gives the results of some species. The differences between the two ways of desiccating is to be attributed to the already mentioned variability of the dispersion. That this may be considerable, appears from the numbers of *Anoetus*. The results do not prove that parallel samples treated differently with respect to the thickness of the layer are incomparable. But there was an important difference in the time of desiccating: the former two samples yielded no further catches after 16 hours, the latter two only after 64 hours.

It is another case if a layer of material, 4-6 cm thick and

lightly piled up, is desiccated, as in the case of the samples of 4 dm³. As compared with the small samples the larger ones always yield far fewer microarthropods. In consequence of the light piling up the slowly moving animals must cover such a long distance that they cannot keep ahead of the desiccation and die in the litter.

The endophagous microarthropods, i.e. those species or stages that eat the substrate from the inside, desiccate in the substrate for the greater part. It is to be attributed to this that so few young specimens of e.g. the Phthiracaridae are caught: JACOT (1939) has determined an endophagous habit of feeding in several species of the latter.

While the desiccation proceeds slowly downwards the animals that love moisture are driven lower and lower. Only when the bottom layer of the sample desiccates as well, the largest numbers of the slowly moving species are caught. This is evident with the slow mite *Nothrus silvestris* which lives in the litter in a great density and with the very small *Oppia neerlandica* (see table 4). Animals moving very quickly fall through the sieve at an earlier moment and are not slowly driven downwards. The cumulation at the end is also very evident in the tables given by TRÄGÅRDH and FORSSLUND: 80-90% of the whole number of animals is not caught before the water contents of the whole sample has decreased to $\pm 15\%$. Unfortunately, the water contents in the upper and lower layers are not determined.

The large number caught in the first hour ought to be attributed to negative phototaxis according to TRÄGÅRDH and FORSSLUND. The mobility is probably also of influence, especially when the sample is spread in a thin layer. Anyhow, it is not generally true of millipedes, beetles and caterpillars, as the authors mentioned think. The very numerous catches of these animals also after the first day show this clearly (see table 5).

Table 5. Catches of some species of the macrofauna of an oak humus sample of 4 dm³ when desiccated slowly by electric bulbs. Beginning of the experiment 8 VIII.
From 22 VIII onwards no animals were caught.

	10 VIII	12 VIII	16 VIII	20 VIII	22 VIII
<i>Lumbricus rubellus</i>	2			3	
<i>Cylindrojulus silvarum</i>			1		
<i>Lithobius calcaratus</i>					1
<i>Campodea staphylinus</i>				5	20
<i>Eosentomon</i> sp.	9	4	6	40	200
Staphylinidae			1		5
id. l.					4
Coleoptera several species l.		1		2	8
<i>Dolopius marginatus</i> l.			1	2	4
Incurvariidae l.	2	1		1	2
Araneina	2	1		1	2

The drying apparatuses used for this investigation accorded in principle with TULLGREN's description. Apparatuses of different sizes were used to desiccate the samples of 40 cm³ and 4 dm³. The most important measures are shown in the following table :

	large apparatuses	small apparatuses
Surface of the sieve :	54 × 54 cm	Ø 27 cm
Mesh width of the sieve :	5 mm	1.5 mm
Distance from the lower part of the lamp to the surface of the sieve :	14 cm	11 cm

In consequence of the scarcity of material the large apparatuses, which like the small ones were made of zinc, were made square so that the funnels had the shape of a pyramid turned upside down. The seams in the funnels appeared to present no difficulty in catching the greater fauna. The large apparatuses were covered with wooden hoods in which four electric carbon filament bulbs could be screwed. The sides of the hoods had large openings covered with fine wire gauze that could be closed with a shutter. This enabled the vapour to escape so that no water condensed in the funnels.

With the small apparatuses there was a sieve inside a 25 cm high cylinder in the top of which an electric carbon filament bulb was suspended, these apparatuses were mostly not closed at the top, so that here too the condensed water could easily escape. The bulbs used in these apparatuses were of 10 or 16 candle-powers. Since the temperature of the room in consequence of heating in winter varied much (from 8°-20° C) the temperature in the desiccating samples also changed. However, it was never higher than 30° C (small apparatuses) and 40°-35° C (resp. in the upper and lower layer of the samples in the larger apparatuses) in the desiccated samples. The temperatures in the desiccating samples were much lower resp. 25° (small), 30°-25° C (large).

Recordings of the temperature in the layer of litter in woods showed maxima of 24° C. Hence the applied temperatures hardly exceed those possible in nature. The time that the samples were heated depended to a great extent on the kind of material and the humidity of the sample. It was always heated till no animals were caught for at least 12 hours. In this way the small samples were always ready in two days, the large ones took 3-7 days. The catching bottles that were fastened at the bottom of the funnels contained a thin layer of liquid of KOENIKE-VIETS (SIG THOR 1931) for the microarthropod samples (a mixture of glycerine, acetic acid and distilled water in a proportion of 11:3:6) and alcohol of about 60% for the macrofauna samples. Of course these methods of conserving were not equally suitable for all species. The integument of small collembolus e.g. often swells considerably in the liquid of KOENIKE-VIETS. Recognition, however, is not made impossible through this swelling. Mites were conserved perfectly in this liquid. Another advantage was that the catches

could be preserved for a very long time in this liquid, without the danger of drying up. Alcohol turned out to be less suitable for worms since they contracted too much in this liquid. Dilution of the alcohol, however, caused strong swellings with beetles and spiders. Especially worms and slugs sometimes clung inside the funnel so that the latter had to be controlled afterwards.

Of course defilement of the catches by litter or humus varied much in the two types of samples, in consequence of the different sizes of the samples and the meshes of the sieves. However, with the chosen sizes of samples and meshes defilement did not prevent collecting quantitatively the animals. Complicated appliances such as the "Ansatzbüchse" of ULRICH were not used: our experience proved that a great part of the microarthropods stayed behind in the rather large quantity of dry litter and humus fallen through the sieves and was difficult to find. Neither were the grates and inserted sieves of JACOT used. He caught the substrate falling through the sieve on a following grate or on a set of sieves placed between the funnel and the catching vessel (JACOT 1936).

The catches of microarthropods were counted in a special dish with a bottom measuring 6×4 cm and sloping sides. The advantage of these sloping sides was that the surface of the liquid was not raised much and was easy to reach with the objective lens. Especially in this edge of raised liquid a great many of the floating small mites and collembolus gathered which would otherwise have been difficult to recognize and to count. In the bottom of the dishes lines were engraved running parallel to the longer sides with interstices of $3\frac{1}{2}$ mm. This distance agreed with the range of vision of the microscope at a magnifying power of $22\times$. With the aid of a mechanic stage the whole dish was searched, the species met with, their stages of development, and their numbers were counted.

The catches of the macrofauna were poured out into petri-dishes and examined, measured and counted with the aid of a loupe with a magnifying power of about $10\times$. As far as they were preserved the catches were conserved in alcohol.

Which part of the animals present in the sample is caught by this method?

In order to be able to answer this question it is necessary to know that, at least for the samples of microarthropods it is not possible to investigate what animals may have stayed behind in the dried samples. It is also very difficult to ascertain the exact number of macrofauna specimens retained in the desiccated samples of 4 dm^3 , as may be concluded from what was explained above in the case of non-desiccated samples. So we are obliged to start from samples with a known number of animals to determine the percentage of caught animals. Therefore samples of litter were desiccated and the animals were caught alive in dishes with natural substrate. In the desiccated samples no living animals remained, as appeared from continued desiccation. The samples were brought again in their original degree of humidity and put into a sieving

apparatus without setting it going. Then a known number of animals was put into the samples. When the animals had got the opportunity to settle in the samples for at least one day, and it had appeared that no animals had fallen into the catching vessel, the bulbs were switched on and the sample was desiccated again.

Table 6. Check of the desiccation method applied on 40 cm³ samples for the quantitative investigation of microarthropods.

The first series of numbers gives the numbers of animals released in different experiments. The second series gives the numbers of animals recaptured in these experiments.

<i>Platynothrus peltifer</i>	2+18+ 1+ 1+ 1+ 1= 24 2+18+ 1+ 1+ 1+ 1= 24 (100%)
<i>Nothrus silvestris</i> ad.	20+20+20+10+50+28+30+30=208 20+20+20+10+43+28+29+28=198 (95%)
<i>Nothrus silvestris</i> juv.	20+20+ 1+20+19+30+30+30+30=200 20+20+ 1+20+19+29+28+22+30=189 (94%)
<i>Hypochthonius rufulus</i>	1+ 1+ 1+ 3+ 1+ 3+ 5=15 0+ 1+ 1+ 3+ 1+ 2+ 5=13 (87%)
<i>Galumna</i> cf. <i>dorsalis</i>	2+ 1+ 2=5 1+ 1+ 2=4
<i>Belba verticillipes</i>	1+ 1+ 1=3 1+ 1+ 1=3
<i>Oribotritia loricata</i>	2+ 1+ 1+ 1+ 6+ 4+ 3=18 1+ 0+ 1+ 1+ 5+ 4+ 3=15 (83%)
<i>Oppia neerlandica</i>	20+15+ 1=36 14+12+ 1=27 (75%)
<i>Phthiracarus borealis</i>	1+ 2=3 1+ 2=3
<i>Trachytes</i> sp.	4+ 2+ 1+ 5+ 3+ 1=16 3+ 2+ 1+ 5+ 2+ 0=13 (81%)
Anoetidae deuto-nymphae	10+ 2=12 8+ 2=10 (83%)
Trombidiformes (> 0.8 mm.)	10 10

For a number of microarthropods the results are clear from table 6. For each species the upper set of data gives the number of the live animals put into the sample, the lower set gives the respective number of animals recaptured. Of course the number of the species is limited and the number of experiments is too small to fix an exact catching percentage for most species. Hence they were not worked into the data of the following chapter. But they do give a clear impression of the reliability of the method. Recatching percentages range from 75% (*Oppia*) to 100% (*Platynothrus*). For some species this method proved unsuitable in consequence of the great mobility of the species: Gamasidae and *Hypogastrura*. Already

before the bulbs were switched on they fell into the catching vessel.

One possibility of loss remains inevitable and uncontrollable: animals that are in a condition of immobility by moulting stay in the sample. Especially with mites that have four stages of development separated by rather long stages of immobility, this factor may be of importance. Possibly this is the reason why FORSSLUND (1948) had better results in his samples of 1 cm³ examined directly with the aid of a dissecting microscope than in the samples of 24 and 100 cm³, desiccated in a Berlese funnel.

Table 7. Check on the desiccation method applied on 4 dm³ samples for the quantitative investigation of macroarthropods

	Released in different experiments	Recaptured in these experiments
Geophilidae	70 + 28 + 35 = 133	62 + 24 + 33 = 119
<i>Julus scandinavicus</i>	10	8
<i>Cylindrojulus silvarum</i>	16 + 10 = 26	16 + 9 = 25
Staphylinidae	4 + 34 = 38	3 + 31 = 34
Elateridae l.	9 + 2 + 2 = 13	9 + 2 + 2 = 13
Coleoptera several species	8	7

The method was also tested for several species of the macrofauna in the same way: table 7. An experiment with 3 × 100 specimens of the larva of *Lycoria sociata* (Diptera) in 3 apparatuses did not yield more than 20, 5 and 11 specimens recaptured. Probably these animals are too delicate for such an experiment. The sometimes very high number of larvae of flies that are caught in a sample makes it plausible that the percentage of the catches in the usual experiments of sieving is rather high. It may vary with different species and different circumstances.

In recatching experiments the reliability of the catching results of *Cylindrojulus silvarum* turned out to be very small at least temporarily. On 23 VI 1947 75 specimens of *Julus scandinavicus* and 75 specimens of *Cylindrojulus silvarum* were put into a dried and again moistened sample of litter in a sieving apparatus. Of the former species, which is very mobile, 65 specimens were already caught the following day; of the remaining ten 9 were caught during the following 3 days. Of *Cylindrojulus* only two of the 75 specimens were recaptured. When the sample was wholly desiccated it appeared that all animals had curled up just above the sieve. Probably the animals tried to avoid the influence of the dryness by a kind of aestivation, as was determined by VERHOEFF (1906) for some species of *Glomeris* and *Brachyjulus*. This makes it necessary to investigate the desiccated sample — especially its lower layer — for these animals. The experiments of recatching done in autumn yielded practically all released millipedes as table 7 shows.

The deviating catching results in frozen samples during winter will be discussed in chapter V C, a 1.

4. Immersing Technique

The quantitative investigation of the not chitinised enchytraeids, nematodes, tardigrads and rotifers is not possible by means of the desiccating technique, as these animals dry up and die or pass into an anabiotic form.

COBB (1918) worked out a method for nematodes in arable soil, based on washing the ground and sieving on sieves with very small meshes. The process is very laborious and not suitable for investigating the litter. A simple method was used by BAERMANN (1917) and after him by many others for collecting nematodes. The technique consists of hanging the sample of soil in a muslin bag in a funnel filled with water and closed by a rubber tube with a screw-clamp. After a day nematodes, enchytraeids, tardigrads and rotifers escape from the sample and sink into the lower part of the funnel just above the clamp. This technique proved to be satisfactory also in gathering nematodes in the litter. Mostly a stone had to be put in with the sample to prevent it from floating. Only a few series of samples were investigated with this technique. The reliability of the results of the catches was not examined.

5. Trap Technique and Recatching Method

A great number of species occurs in too small numbers in samples of 4 dm³ for the purpose of determining their density. A great increase of the number of samples would be necessary to get rather reliable values. Since, in consequence of their small density, most species only play a subordinate part in the community, such increase of the number of samples did not seem worth while.

Of some species we can expect a rather important influence on the community of the litter, in spite of their small density because of their great activity and their predatory way of living. They are a number of beetle species living on prey: Carabidae, Silphidae, Staphylinidae (bigger species), some spiders living at the surface of the soil, Lycosidae, Clubionidae, Lynphiidae and harvesters, Opiliones.

To determine the population density it seemed in principle possible to deduce it from catching results if the effectiveness of the method of catching is known for each species.

The animals mentioned above move very actively across the surface of the soil especially during the period of reproduction. This property was made use of to work out a catching method of which the effectiveness can be determined by means of recatching marked animals, at least for some species. In addition it was possible to trace the phenology and distribution of all species caught by this technique.

At distances of ± 10 m tin boxes were dug up to the rim into the ground, so that the animals fell in when running about. Every day or every other day the tins were emptied and the animals

identified and counted. The boxes used for this trap technique were ordinary biscuit-tins with a surface of 24×24 cm and 25 cm deep. In digging the tins into the ground care was taken to damage the litter surface as little as possible. The litter layer round the boxes was restored to its natural condition as far as this could be done. In order to drain the rain-water an opening was cut in one of the corners of the bottom in which a piece of wire gauze with a mesh-width of 1 mm was soldered. The tins were tilted somewhat so that the opening for draining had the lowest place. The inside was smeared with a very thin layer of vaseline to prevent them from rusting. By means of regular cleaning, the inside remained perfectly smooth so that the majority of the animals caught could not climb up and escape. However, animals with flying power and special climbing power succeeded in escaping. Only if the temperature was sufficiently raised by direct influence of 'sunlight' on the bottom surface of the box, some species e.g. species of *Geotrupes* and *Staphylinidae* unfolded their hind-wings and tried to fly away. On warm and sunny days this diminishes the applicability of the method for the species mentioned, as also the effectiveness of the method is low for climbing species (*Opiliones*, some spiders).

A loss of little importance was the possibility of the animals being preyed upon by fellow-prisoners. This danger was small if the boxes were emptied every other day, while remaining elythra and other chitin rests gave sufficient indication to identify the species. More inconvenient was it when a mouse was caught in the box. Then too elythra would often stay behind, but smaller species were mostly wholly devoured. Since mice could not escape from the box, however, and were mostly found dead, these catches could always be eliminated at the mutual comparison for the dispersal. However, the number of catches eliminated for this reason was very small.

The effectiveness of the catching method differs for the different species. It is plausible that animals with a quick rate of moving will respond less to the presence of a catching box than animals moving slowly. Thus the *Silphidae* *Phosphuga atrata* and *Xylodrepa quadripunctata* moving slowly were never caught in great numbers. Small animals will have an advantage over big ones to be caught: *Lycosidae* and small *Carabidae* e.g. *Notiophilus* sp. were often seen clinging to the edge of the box and returning. Especially of the latter species only a few animals were caught though they have a considerable density and a great mobility. The medium-sized *Carabidae* (e.g. *Pterostichus oblongopunctatus*, *Abax ater*, *Nebria brevicollis*) were caught in great numbers, owing to their size, mobility and density.

There still remain numerous factors that may affect the effectiveness of the catching method for a certain species: e.g. sight and smell, the manner of preying, day and/or night activity. At last in each species the activity, and so the effectiveness of the catching method is influenced by climatological circumstances

(daily and seasonal fluctuations) and by the instinct of reproduction (seasonal fluctuations).

In general, little is known about these properties of the species concerned here. In short, something may be mentioned about what is known of some Carabidae, the most important group caught in this way.

The eyesight is not greatly developed in the Carabidae that were examined in this respect (DELKESKAMP 1930). Whether it is in the other species caught in this way, is not of much importance for the trap technique, since the edges of the trap boxes are wholly camouflaged. According to the same author neither the smell of Carabidae is strongly developed. That Carabidae are not attracted by carrion is evident at the presence of a decomposing dead body of a mouse in a tin. Carabidae, many Silphidae and most of the remaining inhabitants of the soil are not caught in a higher quantity then. This is undoubtedly the case, however, with *Staphylinus chalconcephalus*, *Geotrupes* and *Necrophorus* species, some Silphidae and Histeridae. Some species of the two latter families are even exclusively caught in boxes with carrion. In determining the dispersal of species of Staphylinidae and *Geotrupes* care ought to be taken that the boxes are clean and drain well. Even a few rotting dead beetles are apt to attract great numbers of these beetles.

The preying of *Carabus* species and most of the Silphidae happens "by trial and error" (resp. DELKESKAMP 1930 and HEYMONS et al. 1926—1932) i.e. finding the prey is for the greater part accidental, smell, sight and hearing only function over a very short distance. *Carabus* species especially search preys on the surface (DELKESKAMP 1930). It is evident that this habit of life greatly benefits the effectiveness of the catching method.

Day and night activity of the different species as shown in the catching results will be discussed afterwards (chapter V). It may be a cause of differences in the catches of the species: species that are active both by day and by night may have a greater chance of being caught than species that are active only by night.

The connection between climatological circumstances and daily fluctuations in the catching results of the different species requires a detailed investigation. In general a dependence of the number of animals caught on the temperature could be noticed. Night frost stops all activity, warm and damp nights yield the greatest catches, rain does not affect the activity seriously, continuous drought, however, does.

Seasonal fluctuation in different species as induced by reproduction, aestivation and hibernation will be discussed in chapter V. As regards the activity during the period of reproduction both males and females are very active. The remarkable equality in numbers caught of both sexes in Carabidae will be discussed afterwards. In *Helops laevipectusstriatus* (Tenebrionidae), which was only caught during April and May, the time of reproduction of this species, both sexes were caught in a proportion of

42 males : 5 females. This points to a much greater activity of the males during this time, since in picking out the animals from the litter layer males and females were found in about equal numbers. It is evident that a smaller part of the total population is caught in consequence of the smaller activity of the females than with species where the females are also active. Besides differences in activity between the sexes during reproduction, differences may likewise be expected before and after the time of reproduction. Moreover one-year-old animals may behave in a different way from young ones, which behaviour may affect the possibility of catching them.

All these differences between species and within a species can only be known by studying the life habits of each species accurately. For this the trap technique will no doubt yield important material to be supplemented by observations of animals in terraria.

The differences in activity and other properties mentioned above make it impossible to compare the catching results of different species directly. So determinations of density will have to be made for each species separately.

To determine the population density of some beetle species a method was applied that was first used by LINCOLN (1930) to calculate the density of water-fowls in North America.

The principle is that the proportion of the number of animals ringed during the last breeding season and shot in the following hunting season to the total number of animals ringed may be equalized to the proportion of shot animals to the total population. LEOPOLD (1933) called this proportion "Lincoln-index". Independent of him JACKSON (1933, 1936, 1939) projected a method to calculate the absolute density of the tsetsefly also from the total number of animals caught by means of the proportion between the number of marked animals released and the number recaptured. He worked with a population in which continually birth and mortality and moreover emigration and immigration could take place. By an ingenious method of marking these four factors could be calculated separately.

DOWDESWELL, FISHER and FORD (1940) also investigated the daily change in the total number of butterflies in an isolated colony of *Polyommatus icarus* Rott. with the aid of the Lincoln-index by daily catching, marking and releasing the animals. Birth, mortality and total number of animals in the colony could approximately be estimated.

FISHER and FORD (1947) applied the same method during six successive years in investigating the yearly population changes in an isolated colony of *Panaxia dominula* L. The daily number of butterflies was fixed supposing constant mortality and from this the population was estimated for each year.

In applying the Lincoln-index to beetles caught in catching boxes we must be able to dispose of sufficiently large catches.

Hence it is only possible to apply the method to animals occurring in a sufficient density during the period of their greatest activity. The method was only applied to a few species viz. *Pterostichus oblongopunctatus*, *Abax ater* and *parallelelus* and *Staphylinus chalconcephalus*. The other species were caught in too small a quantity to be marked in a sufficient number. The two species of Lycosidae were caught in a sufficiently high number during their reproduction period but I did not succeed in marking the animals in such a way that the mark remained permanently without harming the animals.

Primarily in marking, both spiders and beetles got a mark of a colouring matter suspended in an alcoholic shellac-solution. In the long run the colour-mark appeared not to be proof against the creeping in and across the litter of the animals, so that another way of marking was thought of. Marks of Canada-balsam appeared to be resistant but it was very difficult to prevent the animals from getting it on their legs, when it was drying, which made them unfit for experiments. Finally in the case of the beetles the most satisfying method was to cut off a small part of one of the hind-wings. The beetles did not experience any trouble and the operation could be performed very quickly. The unprotected part of the abdomen was so small that a greater chance of attack by predators was not probable. Kept together with congeners and larger carnivorous beetle species the marked specimens were not attacked in a larger number than the not-marked ones.

The calculation of the population density was based upon recatching marked animals released on a certain date and distributed equally over the whole experimental area. Is the number of marked animals released M , the number of marked animals caught on an arbitrary date m and the number of not-marked animals caught on that date n , then the total of the not-marked animals present on the day of releasing (N) is : $N = \frac{nM}{m}$, if the following conditions are fulfilled :

1. No new animals hatch during the course of time between releasing and recatching the animals.
2. Eventual mortality takes place at the same rate with marked and unmarked animals, while activity is the same in both groups.
3. The released marked animals do not leave the experimental area in this course of time and no immigration nor emigration takes place in the autochthonous population.

If new animals hatch between releasing and recatching the marked animals, the total number of animals caught becomes larger than this would be otherwise. The calculated population density on the day of releasing becomes larger. Only when no young animals hatch (recognizable by weak hind-wings) this method may be applied. So in the latter part of the summer in consequence of the hatching of the new generation no reliable density calculation is to be performed of *Pterostichus oblongopunctatus* in spite of sufficiently large catchings.

Mortality during the catching period, lasting for only two or three weeks, is considerably smaller for Carabidae and Staphylinidae with their long adult life time (1—3 years) than for flies and butterflies, the life time of which is only a few weeks. Mortality, however, does not affect the population density calculated, as the relation n/m is not affected. This would be the case if the marked animals were liable to greater or smaller mortality. Observations of animals in captivity did not yield any difference, however, between marked and unmarked animals.

To have a sufficient number of marked animals at hand it was required in the case of *Pterostichus* and *Abax* to keep the animals alive in a terrarium for some time, which can be done with flies, worms and pieces of meat as food. The influence of the time of captivity on the activity of released animals was examined for *Pterostichus* and *Abax*. Two series of 90 marked specimens of each species kept in captivity resp. less than a week and longer than a month, were released during their reproduction period. The numbers of animals recaptured in three weeks are collected in table 8.

Table 8. Recatchings of *Pterostichus* and *Abax* kept in captivity for different periods.

		number released	number recaptured	% recaptured
<i>Pterostichus</i>	< 1 week	90	19	21.1
Idem	> 1 month	90	16	17.8
<i>Abax</i>	< 1 week	90	10	11.1
Idem	> 1 month	90	14	14.7

In neither of the two species a significant difference between the recatches is noticed. Had there been any influence of the captivity on the activity after releasing it had, no doubt, been stronger after more than a month's captivity (6 weeks on an average) than after less than a week's (3 days on an average). Since this is not the case the influence of captivity on the activity seems improbable.

If the activity of the marked animals after releasing was considerably lower or higher than that of the autochthonous ones this would appear in the proportion between the number of unmarked autochthonous animals in the first catches after releasing the marked animals and the number of marked animals recaptured in the same catches. With a higher activity of the marked animals released they would at first be caught in a relatively larger number than the autochthonous unmarked animals, with a lower activity in a smaller number. Below (p. 41 and fig. 2) we shall see that this proportion is not essentially higher or lower in the first catches than that in the subsequent catches. So there is no reason to assume a deviation in the activity after releasing.

The third condition for a reliable determination of the population density is that the animals will not leave the experimental area and no animals from the surroundings enter. It stands to reason that this condition is

only to fulfil by fencing in the experimental plot by a proof enclosure. Even an enclosure of zinc about 15 cm high, put into the soil could not quite prevent a mutual exchange. Marked animals in a surface of 16 m², wholly surrounded by zinc strips, were caught outside the enclosure after some weeks. The only exact method seems two furrows with steep walls surrounding the experimental plot, the inner of which catching the animals leaving the plot, the outer one catching the animals trying to enter the plot from the adjacent area. The furrows have to be made on the same date that the marked animals will be released, since the inner furrow functions as a trap for marked and unmarked animals on the plot. Application of this method however was not possible in this investigation.

Without any enclosure migration of the animals during the catching period is unavoidable. If the experimental surface does not attract nor repel the animals during the catching period, immigration and emigration of unmarked animals will counterbalance each other. The only reason to assume any special attractive working during catching is the decrease of local density by which animals from the surrounding area may be attracted. Another factor disturbing the proportion of marked and unmarked animals is emigration of marked animals. Both immigration of unmarked animals and emigration of marked animals during the catching period cause increase of the ratio n/m and overestimation of the population density. Does this ratio increase to such extent that it prevents calculation of approximate values for population density from the numbers of marked and unmarked animals caught?

To know this experiments with *Pterostichus*, *Abax* and *Staphylinus* were taken, the results of which are presented in fig. 2. This figure shows pictures of the absolute quantity of catches and recatches of these species in boxes on distances of 10 m during a catching period of 18 days in which time the animals caught were counted every other day. In these graphs the data of two catching periods are combined. The normal lines indicate the values of an 18 days' period in the beginning of July 1946 in the oak forest 8 H and the heavy lines indicate the values of an 18 days' period in the beginning of August 1946 in the beech forest 8 G.

In both cases 180 specimens of *Abax* and *Pterostichus* were marked and released (evenly distributed) in the experimental area of 30 × 60 m. In the first case 100 marked specimens and in the second 90 marked specimens of *Staphylinus* were released too. The long lines show the catches of unmarked animals, the short ones at their base the recatches of marked animals and the figures below these lines indicate the proportion between the two. The pictures show that in no species the succeeding proportions have a tendency to increase. Nor the proportions of the first catches are significantly higher or lower than those in the other catches (p. 40).

The small catches of *Pterostichus* during the second period can be explained by the fact that the reproduction period of this species is over at that time. In consequence of these small catches the

recatches are high in proportion to the catches but they do not show a tendency to decrease. In the case of *Staphylinus* the proportion of catches and recatches has a rather high value on the first catching day, caused by the large catch of unmarked animals at the second experiment for which no explanation can be given. Decreased activity of the animals released is, however, not to conclude from this: the other first catch and the two second catches present normal proportions.

So these data indicate that in an area of 1800 m² emigration of marked and immigration of unmarked animals does not take place in such a rate that it greatly affects the calculation of population density.

From the above it is clear that the values of the population

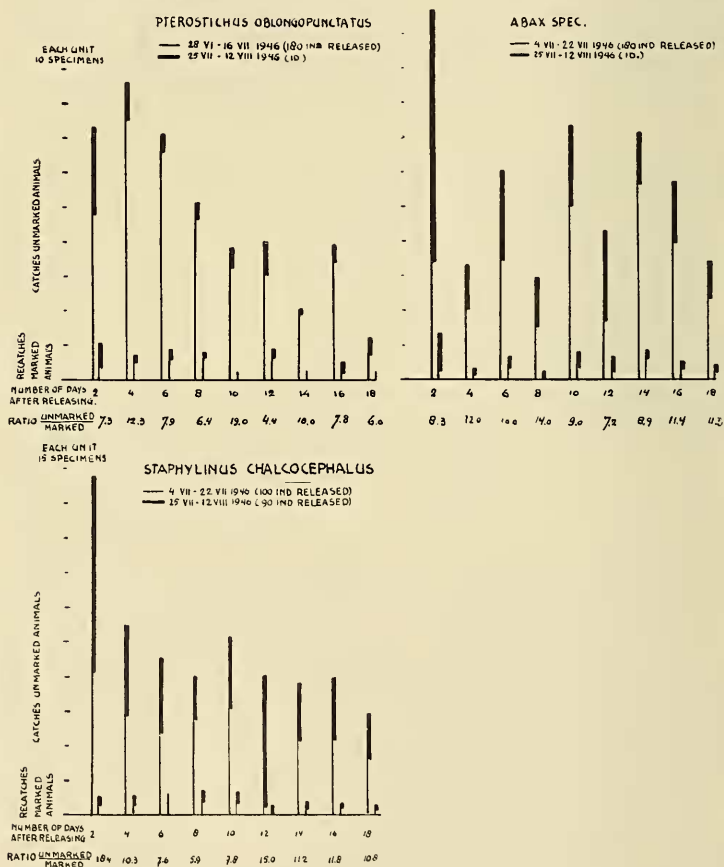


Fig. 2. Comparison of catches of autochthonous animals (unmarked) and recatches of released animals (marked) during 18 days after releasing the marked specimens (two experiments on plots of 18 a).

density are not very exact. The most important part of the trap technique without any enclosure is that it enables us to acquire knowledge of the qualitative composition of the epedaphic macrofauna, gives us data about the dispersion over the area and about the seasonal periodicity of the different species and moreover enables us to determine the approximate values of the population density.

In choosing the experimental area for the determination of the population density, that part of the area will satisfy most where the population density is homogeneous and rather high. From the value of the density found here we can calculate the density in other parts of the area if the density proportions are known of these parts and the plot investigated. The dispersal can be fixed by providing the whole biotope with catching tins regularly distributed at equal distances of 20-40 m dependent on the size of the biotope, the expected heterogeneity and the time at one's disposal. After catching for a period of 1-3 weeks, varying according to density and activity of the species a dispersal map can be made from the catches in the different boxes. As local concentrations of a particular species lead to locally higher catches, the number of animals caught is an indication of the density on the spot. In fig. 13 the dispersal has been given of a number of species in and around the beech forest 8 G deduced from the catching results during a period mentioned for each species.

The dispersion appears to be irregular for most species even within the forest (inmost rectangle in each figure). That this dispersion is not a temporary one is shown by the comparison of the results of *Pterostichus* caught during five different periods in boxes at respective distances of 10, 10, 20, 20 and 40 m.

Also in other species the dispersion shows a great conformity at different points of time so that it is clear that a high active dispersion is not probable in these species, for this would be expressed in changing dispersion maps.

The density determination of *Pterostichus*, *Abax* and *Staphylinus* which were performed in a young oak forest in the beginning of July 1946 may be used as an illustration of the method dealt with (table 9).

On 28 VI 1946 27 boxes were dug into an experimental area of 60 × 30 m. Up to 22 VII 1946 the catches were removed every other day. On 28 VI 180 specimens of *Pterostichus oblongopunctatus* were released and regularly spread over the area, half of them were kept in captivity less than a week and marked on the right, the other half were kept in terraria for more than a month and marked on the left. On page 40 we already saw that there was no difference between the recatches of the two groups so that the two series may be regarded as duplicates. Of the two *Abax* species, *ater* and *parallelus*, which only later on were discerned as different species, the same numbers with the same marks and treated in the same way, were released on 6 VII and at the same time also 100 specimens of *Staphylinus chalcocephalus* (kept less than a week in captivity) only marked on the right.

Table 9. Population density in numbers per a of *Pterostichus oblongopunctatus*, *Abax ater* and *parallelus* and *Staphylinus chalcocephalus* in a young oak forest (8 H). Densities calculated from added and individual data from 30 VI (6 VII) to 22 VII 1946.

	Date	caught unmar- ked(n)	Recaptured marked(m) r l r+1	Population density per a (N)					
				added data			individual data		
				r	l	r+1	r	l	r+1
<i>Pterostichus oblongopunctatus</i> .	30 VI	48	3 — 3	80	—	160	80	—	160
	2 VII	75	2 3 5	123	205	154	184	128	150
	4	66	3 3 6	118	158	135	111	113	112
Released on a plot	6	46	4 2 6	98	152	118	63	118	81
of 18 a (M): 90 ind.	8	32	1 1 2	103	148	121	152	159	155
r (less than a week	10	30	3 3 6	93	124	106	58	60	59
in captivity), 90 ind.	12	19	2 — 2	88	132	105	56	—	97
1 (more than a month	14	34	— 2 2	97	125	109	—	91	159
in captivity).	16	7	— — —	99	128	112	—	—	—
	18	10	— 1 1	102	122	111	—	60	100
	20	9	— — —	104	125	114	—	—	—
	22	7	1 1 2	101	120	109	49	50	50
				Average			94 ± 17.8	97 ± 13	112 ± 14.8
<i>Abax</i> sp.	6 VII	35	1 1 2	175	175	175	175	175	175
	8	20	1 — 1	138	275	183	101	—	199
Released on the	10	34	1 2 3	148	148	148	169	87	115
plot: the same num-	12	15	— — —	173	173	173	—	—	—
bers as in <i>Ptero-</i>	14	50	3 1 4	128	192	154	84	247	127
<i>stichus</i> .	16	17	1 1 —	122	171	143	288	89	89
	18	56	1 5 6	142	114	126	268	62	97
	20	39	1 3 4	148	102	121	190	70	100
	22	24	1 1 2	145	103	121	123	117	120
				Average			150 ± 22.3	121 ± 25.4	128 ± 13.9
<i>Staphylinus chalco-</i>	6 VII	62	4	86			86		
<i>cephalus</i> .	8	43	4	73			61		
	10	50	9	51			29		
Released on the	12	41	7	45			36		
plot: 100 ind. r	14	47	5	47			51		
(less than a week	16	3	—	42			—		
in captivity).	18	31	2	50			75		
	20	41	3	52			67		
	22	23	1	54			102		
				Average			63 ± 8.7		

The density can be calculated in two manners. By adding the catches and recatches of each date to those of the preceding dates the original population can be calculated on the succeeding dates with increasing exactness, for it is based on a successively higher number of catches. Using the same symbols as on p. 39 and S being the surface of the plot expressed in a (are = 100 m²) then the population density in numbers per a on the date of releasing, calculated from the first catching is $N = \frac{n_1}{m_1} \times \frac{M}{S}$. The density calcu-

ated from the first and second catching is $N = \frac{n_1 + n_2}{m_1 + m_2} \times \frac{M}{S}$.

The most probable density is calculated from all data: $N = \frac{\sum n}{\sum m} \times \frac{M}{S}$.

The duplicate data of *Pterostichus* and *Abax* generally agree rather well. In the beginning the values calculated from the total number of marked animals recaptured (r and l) show rather high differences (to be ascribed to the small number of catches) but they get already a stable value after about a week.

The original population is also to be calculated from the separate catches of each date. Then we must make allowance for the number of animals marked and not-marked caught in the preceding days by subtracting the marked and adding the not-marked. The first catching naturally gives the same calculation as in the preceding method. The second catching gives:

$$N = \frac{\frac{n_2 (M - m_1)}{m_2} + n_1}{S}$$

The third catching:

$$N = \frac{\frac{n_3 (M - m_1 - m_2)}{m_3} + n_1 + n_2}{S} \text{ etc.}$$

Of course these data vary much more than the values calculated from the added data, while no values are to be calculated of the days that no marked animals are caught. They have the advantage that from the data an average with a standard error can be calculated. The found values in general agree rather well with those obtained by the other calculation method.

The experimental period was rather late for *Pterostichus*. The decrease of the catches after 14 VII points to the fact that the reproduction period was over. Therefore the values calculated after that date are based on too low numbers to be of much value.

In this case the population density was determined without separation of males and females. However it is quite possible that the two sexes do not behave in the same way as regards their active dispersion and so leave the experimental plot in a different rate.

To find this out on 16 V 1947, that is during the reproduction period of *Pterostichus oblongopunctatus*, 120 marked males and 120 marked females of this species were released, evenly spread over a surface of 1200 m² (30 × 40 m) in the most densely populated part of the beech forest 8 G. Here 12 tins were dug at distances of 10 m each. Around this experimental plot there was a network of 20 catching boxes at distances of 40 m which made it to some extent possible to examine the eventual dispersion of the marked animals over a large area.

During a fortnight catches were made and — distinct from the

preceding case — both marked and unmarked animals were released after counting. By this the number of marked animals in the field remained as high as possible and the second calculation method was simplified, the population density being $N = \frac{nM}{mS}$.

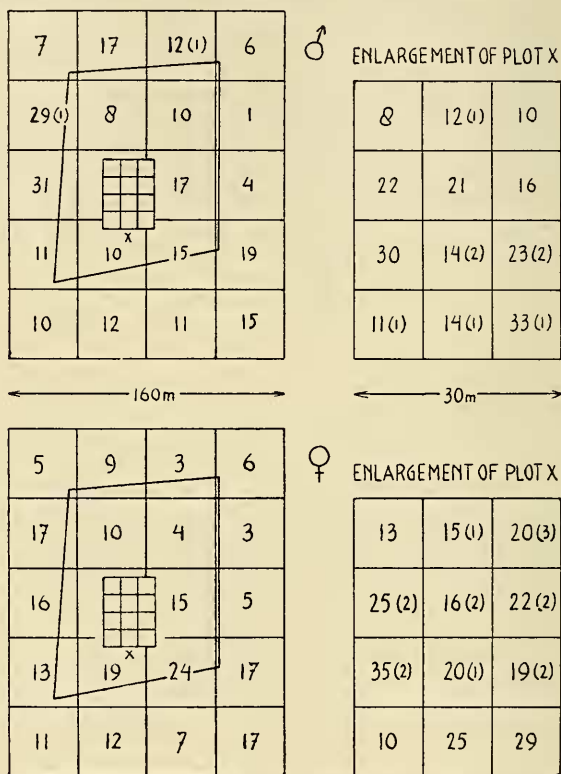


Fig. 3. Distribution of *Pterostichus oblongopunctatus* males (top) and females (bottom) in beech forest 8 G. 16 V — 30 V 1947. In parentheses: numbers of marked beetles released on plot X.

Fig. 3 shows the dispersion of males and females over the whole area and over the experimental plot. The numbers in parentheses are those of the marked animals recaptured. Table 10 shows the catches on the different dates and the densities calculated. From the data it appears that 2 males and no females were recaptured outside the experimental plot to 8 males and 15 females inside it.

Though the numbers are very small they may indicate a larger active dispersion of the males. This is affirmed by the fact that within the experimental plot 214 unmarked males were caught to 249 unmarked females while this proportion was 244 : 212 outside it. In applying the chi-square-test to these numbers this difference,

Table 10. Catches and recatches of *Pterostichus oblongopunctatus* on an experimental plot of 40 x 30 m [S = 12] and on the surrounding area in the beech forest 8 G.

	Males					Females				
	on the experimental plot			on the surrounding area		on the experimental plot			on the surrounding area	
	un-marked (n)	marked	density per a (N)	un-marked	marked	un-marked (n)	marked	density per a (N)	un-marked	marked
Released: 16 V '47		M=120					M=120			
Caught:		m					m			
17 V 7.30	23	—		18	—	19	1	190	4	—
17 V 18.30	9	—		9	—	9	—		5	—
19 V	20	3	67	27	—	16	—		14	—
21 V	34	1	340	42	1	56	5	112	37	—
23 V	29	1	290	32	1	49	1	490	45	—
27 V	66	3	220	116	—	54	4	135	107	—
30 V	33	—				46	4	115		

in fact, appears to be real ($P = 0.027$). In consequence of chance this would only occur in 27 of a 1000 cases.

From the catching data the densities, expressed in numbers per a were calculated both for males and females. That these values are higher for males than for females is chiefly the consequence of the smaller recatches of the marked males and this in turn of the larger dispersion of the males outside the experimental plot. The most probable value of the density of the species is about $13/7 \times$ the density of the females (catches males : females within the experimental plot = 214 : 249). Thus the total density may be estimated on about 250 per a.

CHAPTER IV

DESCRIPTION OF THE ENVIRONMENT

1. The Area of Investigation

During the Riss-glacial the Netherlands were covered with an ice-cap up to about the line Haarlem—Utrecht—Nijmegen. The most southern tongues of this ice-cap penetrated into the existing river valleys of the preglacial landscape and drove up the terrace-walls in this way. Valleys and terrace-walls were covered with a layer of boulder-loam, which when the ice melted, got covered with fluvioglacial depositions for the greater part consisting of fine-grained sands. Whether these fluvioglacial depositions have been able to hold their own till now or, in consequence of "drift" erosion, have disappeared and have been substituted by erosion material originating from the preglacial ridges, as EDELMAN and OOSTING suppose, it is a fact that the preglacial ridges are surrounded by a coating of fine-grained sands that we will call fluvioglacial sands

here, conformably to the geological map of the State Geological Service.

On these fluvioglacial sand areas sand drifts arose, which according to the dominating S.W.-winds lie in a S.W.-N.E. direction.

The National Park "De Hooze Veluwe" in the N.E. part of which our area of investigation lies, is almost wholly situated on these fluvioglacial sands. The sand drifts were restricted by afforestation of the surroundings to some areas only. In the East and the South the Park is bounded by the large preglacial ridge forming the East of the Veluwe.

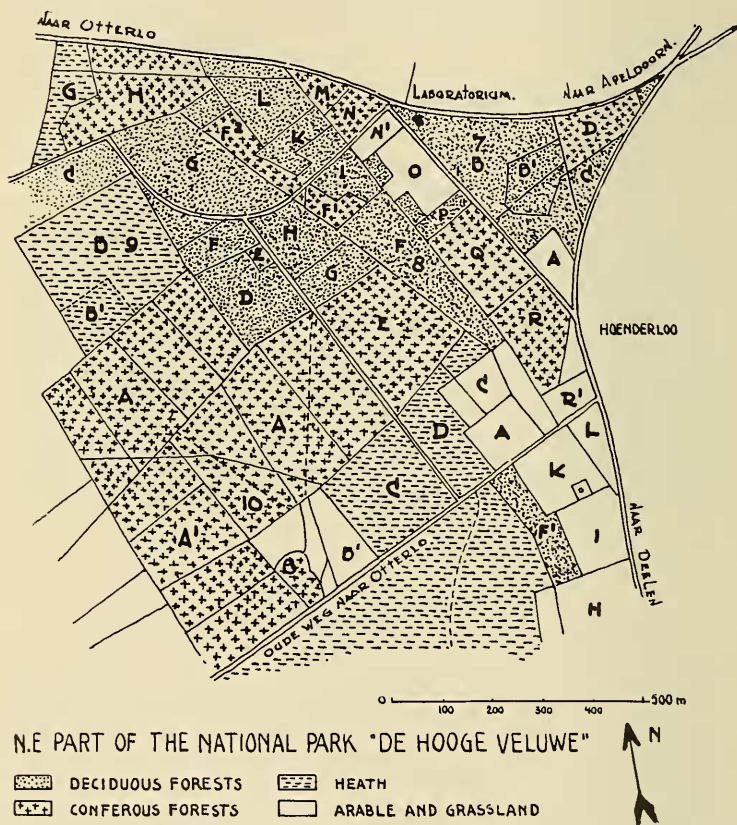


Fig. 4. Map of the experimental plot 8 G and its surroundings (Naar = to ; coniferous read coniferous).

The N.E. part of the Park (fig. 4) is situated on a transition of preglacial to fluvioglacial material, fine- to middle-grained sands mixed with fine gravel, in which larger stones are also often found.

The area, at first overgrown with heather was partly afforested with beeches and oaks between the years 1860 and 1880. The soil

was dug up to a depth of 1 m and the heather profile was buried by a sand layer greatly differing in thickness (4-20 cm). This sand layer has only changed little by the culture of hard woods: the upper few cm were leached especially under the influence of the slowly decomposing beech litter, while parts of humus were washed into this layer or, to a slight extent, brought down by animal activity. The surrounding fields afforested with Scotch pine about 1887, were not dug to such a depth and show a hardpan everywhere 10-20 cm thick. In the plots 9 D, 9 F (except the most northern part), and in the southern part of 8 G remnants of this hardpan occur. The other plots situated more northerly at best show an illuvial layer dark-brown in colour. Often, however, it is mixed with sand from the parent layer and the eluvial horizon in which a dark brown nuance is visible then.

The beech forests, nearly all of them mixed with oaks, have practically no undergrowth. The decomposition of the litter takes place very slowly with the exception of some parts of the plot 8 K, and accordingly causes the formation of raw humus everywhere. The greater part of the oaks have been regularly cut down for gaining tannins. The shoots from the stumps have not been cut down the last few decades and have developed into lank trees. The plots in which the oak dominates show a poor undergrowth of the association belonging to these soils: *Querceto-Betuletum* typicum. Here the decomposition of the litter also causes the formation of raw humus, though to less degree than in the beech forests. Where an old beech stands in these forests we meet a considerably thicker humus layer. The plots of Scotch pine stand on a podsol profile with a leached horizon of 20 cm thick and a hardpan only a little less thick. The soil has not been dug and the profile is practically not changed by the influence of the forest vegetation. In these forests a dense brushwood has developed in a natural way, consisting of *Quercus robur*, *Betula* sp., *Quercus borealis*, *Sorbus aucuparia*, *Frangula alnus* and *Prunus padus*. The decomposition of the litter is very slow: the soil is covered with a mass of needles overgrown with the moss *Pleurozium Schreberi*, and in lighter places with *Vaccinium Myrtillus*.

The most important experimental plot, the beech forest 8 G (see fig. 5), must be described somewhat more in detail¹⁾. The whole plot has a surface of 1 ha (= $\pm$ 2.5 acres) and slopes slightly to the N.E. The greater part of the plot is occupied by beeches and oaks, about 85 years old, planted in rows (S.W.-N.E.) at distances of $7\frac{1}{2}$ m. The beeches have at breast-height an average outline of 172 cm (extremes of 135 and 224 cm). They branch very strongly at 3-5 m and are about 20-22 m high. The few oaks left between the beeches were suppressed by them and grew up rather straight and high. The average outline of the trunks is 103 cm and they have the same height as the beeches. Between these trees several groups of slender oaks are found about 40

¹⁾ For photograph of this forest see opposite p. 1.

years old, shot up from oak-stumps. They have a length of 15–17 m and an outline of the trunk of only 36 cm. Both the old oaks and the shoots only yield a very small part of the annual litter, so that the surface of the litter, except under the remaining oaks, practically consists of beech litter only. Undergrowth is wholly wanting in this part. Only on old dead stumps of oaks we meet a vegetation of moss chiefly consisting of *Dicranum scoparium*. To this part of the plot the present investigation is mainly restricted.

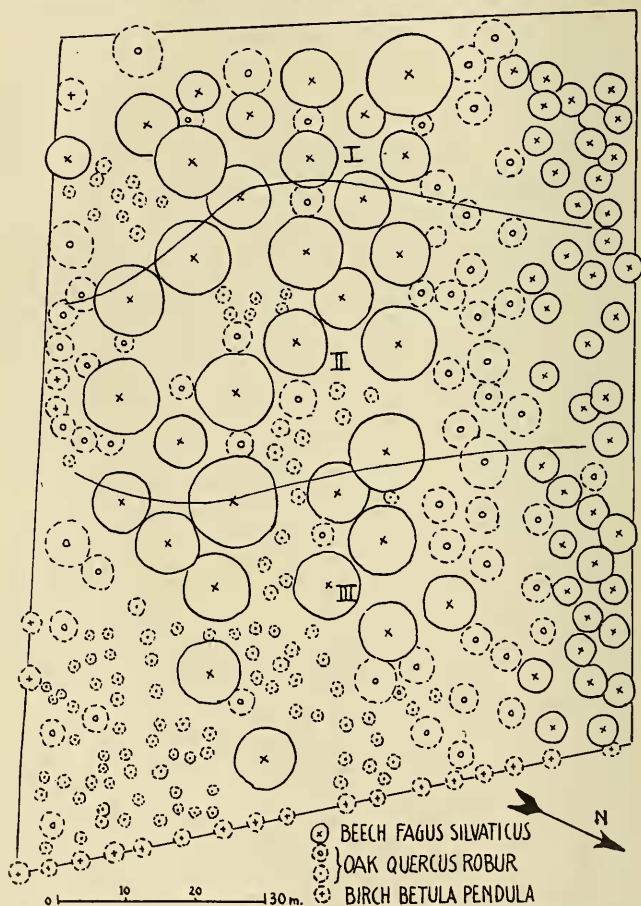


Fig. 5. The experimental plot: beech forest 8 G. I, II and III different floor-types.

Along the S.E. border the forest consists of old oaks with some oak-shoots and beeches, birches and *Sorbus* in the southern corner. The cover of the layer of trees is only 5% here; under it a thin vegetation of herbs has developed (covering 5%) consisting of *Vaccinium Myrtillus*, *Deschampsia flexuosa*, *Luzula campestris*, and some seed-plants of beech and red oak. The moss layer covers 70% and consists of *Polytrichum attenuatum*, *Leucobryum glaucum* and *Cladonia* sp.

The N.E. part of the forest chiefly consists of 40 years' old oak-shoots with an average outline of the trunk of 44 cm and a height of 10–15 m. The eastern corner contains a vegetation of bushes covering about 20% and consisting of the species mentioned above. The moss layer covers 60% and consists of *Polytrichum attenuatum*, *Dicranum scoparium*, *Hypnum cupressiforme*, *Pleurozium Schreberi* and *Aulacomnium androgynum*.

The N.W. part of the forest is formed by two strips about 15 m broad, both parallel to the planting direction of the 85 years' old beech forest. One is covered with oaks about 60 years old, the second with beeches of the same age. Both oaks and beeches are slender and have a height of 19–20 m. The oaks have an average outline of their trunks of 103 cm, the beeches of 113 cm. Except on a surface of $\pm 200 \text{ m}^2$ in the S. W., with an almost uninterrupted vegetation of *Leucobryum glaucum*, *Polytrichum attenuatum* and *Dicranum scoparium*, here too any undergrowth is absent.

The S. W. side of the forest is bordered by a 10 m broad strip of red oaks and birches. The herbaceous layer at their foot covering 70% consists of *Calluna vulgaris* with reduced vitality, seed-plants of beech and oak, *Vaccinium Myrtillus*, *Deschampsia flexuosa*, *Luzula campestris*, *Molinia coerulea*, *Poa nemoralis*, and *Lycopodium complanatum*. The moss layer is badly developed, only consisting of *Polytrichum attenuatum* and *Pleurozium Schreberi* in some places. This strip borders again to a broad forest-road.

In the S. E. and N. E. the plot is bounded by a wall 50 cm high and ± 1 m broad. The first wall (S.E.) has some old birches; the brushwood-, herb- and moss-vegetation agree with the vegetation of the neighbouring parts of the plot. On the outside of this wall is an old forest-road overgrown with red oak-shrubs, birches and beeches of 1–3 m high. The herbaceous layer consists for the greater part of *Vaccinium Myrtillus*, *Molinia coerulea*, and *Calluna vulgaris*. The N. E. wall bears a row of birches of 12 m high, under which a vegetation of brushwood of oaks and red oaks, covering 20%. The vegetation of herbs and moss only covers a small part and consists of the same species as are found under the oak-shoots in the N. E. part. On the outside of this wall of birches runs a narrow foot-path, on the other side bounded by an afforestation of 15–20 years' old red oaks wide apart. Except some shoots of red oaks and *Frangula alnus*, here we find a vegetation of *Calluna vulgaris* covering 30%, while the moss layer up 90% and exclusively consists of *Pleurozium Schreberi*.

The N. W. side of the plot is bordered by a forest of red oaks 17 m high and very much thinned in 1946 in consequence of damage caused by shell-fire sustained during war activities in April 1945. Upon the stumps quickly growing shoots have sprung up. The surface is covered with a thin hard layer of litter, on which nitrophile grasses have locally developed. To the N. E. this forest passes into an oak-shoot forest about 45 years old. Here the undergrowth agrees with the places with oak-shoots described above.

About the profile under this plot it was already mentioned above that it was greatly influenced anthropogeneously. In the S. W. part we find remnants of the brown hardpan horizon of the old podsol profile at a depth of 50–60 cm; more to the north in this plot we find these remnants nowhere; only the grey podsolized sand covered with a layer of sand from the underground we find everywhere.

Remarkable is the very small influence of the 85 years' old layer of litter on the substrate. It is restricted to the upper 3–5 cm of the sand layer and consists in leaching the sand grains, which lose their films of iron compounds and in washing down humus particles, which mixed with quartz grains, give the whole layer a black-grey colour.

The granular composition of the substrate and its humus content were determined by the Soil Testing Laboratory at Gro-

ningen of the National Council for Agricultural Research T.N.O. and appear from fig. 6. In the three layers the sand must be qualified moderately fine with a moderate silt content. It is obvious that the underground brought upwards is somewhat coarser than

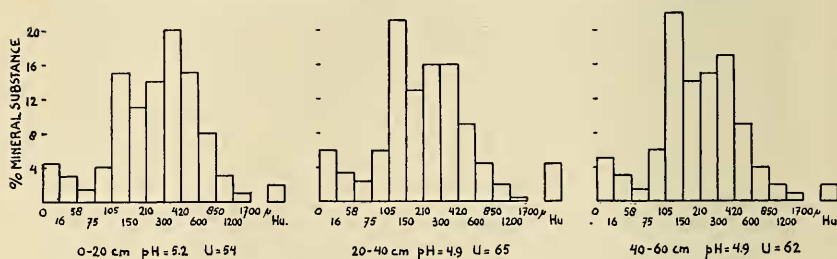


Fig. 6. The granular composition and humus content of the mineral substrate on different depths in the beech forest 8 G.

the other two layers. The humus content in the old podsol horizon is more than twice as high as in the other layers.

2. The Forest Floor

The forest floor, defined in accordance with the Third International Congress for Soil Science in Oxford (1935) as: the whole of the organic material on the soil surface (including litter), has differently developed in the different parts of the forest.

Before, however, we pass on into the description of the forest floor, it is desirable to discuss the terminology of the layers to be distinguished separately. In the literature this terminology is often confused with the general types of forest humus formed under the influence of climate, substrate and soil organisms.

In 1878 P. E. MÜLLER already distinguished two types of forest humus: mull and mor. In the mull, under the influence of bacteria and a rich fauna of earthworms, a decomposition of the litter takes place, keeping pace with its yearly supply. The humus formed is mixed with the mineral substrate and causes a loose crumbly structure here. In the mor-type the decomposition is chiefly the work of moulds and of a fauna in which the large species are lacking. The humus layer forms a thick coating on the mineral soil and is hardly mixed with it. However, this biological view of MÜLLER was lost sight of. Under the influence of soil scientists such as GLINKA, EHRENBURG, and WIEGNER, the electrolytic colloidchemic view came to the fore.

In 1935, however, through ROMELL, HEIBERG, and BORNEBUSCH the old classification in two principal types based on morphological qualities was accepted at the 3rd International Congress of Soil Science in Oxford and the two types were divided into three subtypes. For this investigation only the mor-type is important. This was divided into:

1. Granular mor. The humus layer is well developed, of a fine

granular structure, and the lower part is somewhat more compact. In dry condition it is easily broken into fine powder when pressed by hand.

2. Greasy mor. The litter layer is usually not much developed and is more or less fibrous. The humus layer is thick and compact, when wet distinctly greasy to the touch, when dry hard and brittle.

3. Fibrous mor. The litter layer is well developed. Litter and humus layers are fibrous, but not compact. In the humus layer many remnants of plant are visible.

The differentiation of the separate layers in a mor-type originates from HESSELMAN (1926). He distinguished an F layer (= förna- or fermentation layer) and an H layer (= humus- or heavily decomposed layer). The F layer consists of more or less decomposed litter, still recognizable as such and with a loose structure. The H layer mainly consists of fine divided organic material, more or less dense; the original structure of the litter is not to be recognized, though in the dark amorphous humus mass still fragments of litter may occur. This classification, which is in common use, will be applied here too.

The loose litter layer, in general originating from the last autumn will be indicated as F_0 , further we might distinguish an F_1 , F_2 , F_3 layer etc. F_1 is the litter of the last autumn but one, which is more or less compressed and is kept together by moulds, its original leaf-structure is rather well recognizable in spite of reduction; F_2 and F_3 is the litter resp. 2 or 3 full years present in the forest floor. These layers are to be distinguished separately in places with a very slow decomposition and in the absence of disturbing influences such as high winds and frequent treading of man and animal. As a guide in identifying the different layers in beech forests, the empty cupuli can be used that are very abundant in some years, and nearly absent or scarce in others. In general the layers under the F_1 are, however, not separately distinguished. They pass into each other without distinct difference and form together a homogeneous layer that we will call the F_x layer here. This F_x layer gradually passes into the humus layer, the H layer. The latter often contains litter fragments that are still recognizable even without magnification. Downwards the number of these litter fragments decreases very much; we consider the H layer to start where the organic material consists of at least 50% amorphous humus.

Under this coating of organic material lies the inorganic material. As far as this is leached by climate and floor and thus has lost its soluble elements, it is indicated as A_1 (eluvial horizon). For our purpose only the upper layer directly influenced by the floor is important. It consists of leached mineral grains mixed with parts of humus, washed into it by rain. The colour of the layer is dark-to light-grey, dependent on the humus and water content. Both upwards and downwards the limit is rather distinct.

Now let us consider the floor of our experimental area. Im-

mediately after the falling of the leaves the F_0 layer is a layer of a loose structure about 5 cm high. Besides the leaves of the beeches and the oaks of the plot there appear to be some leaves of red oak blown in from the plot adjoining the experimental area to the N.W. The beech leaves predominate, however, as an analysis of the weights of 16 samples of 0.5 m² of litter collected a week after falling will show (table 11). Only in 6 out of 16 samples oak leaves were

Table 11. Composition of the F_0 litter after leaf fall in 1947 in the beech forest 8 G, derived from 16 samples each of 0.5 m².

	Average weight (air-dry) in g per 0.5 m ²	Composition in % (rounded off)
Beech leaves . . .	205 (147—266)	78
Oak leaves	5 (0—17.5)	2
cupuli.	21 (2—81)	10
twigs	32 (6—68)	12
total average . . .	262	

found. Even in the neighbourhood of the oaks the oak leaves does not amount to more than $\pm 6\%$ of the total quantity of the F_0 litter. In the spring of 1947 a wholesale shift of the F_0 layer in a N.E. direction could be observed, caused by the high S.W. wind that had free scope under the leaveless trees. Consequently the F_1 layer came to the surface in the S.W. part, whereas in the N.E. part the F_0 litter had locally heaped up to 8 cm high. To the wall forming the N.E. borderline the F_0 layer was even 10-15 cm high. Though such a shift of litter does certainly not take place every year, the F_0 material is indeed often blown by spring storms in a N.E. direction.

The composition of the floor is often different on very short distances. In spite of these local differences it is possible to distinguish three types gradually passing into each other (fig. 5 I, II and III, p. 50).

The first type (I) occurring in the most S.W. part of the forest and in some places bearing 40 years' old oak-shoots is most like the greasy mor-type. It consists of a very thin compacted F layer (to 1 cm) formed by small litter fragments (± 1 cm²) with few animal excrements, many brown mould hyphae covering the litter fragments with a dense net-work, and numerous mycorrhizas. The H layer under it is 3-4 cm high, very compact, black, amorphous, with many tree roots but few mycorrhizas; in the upper part a good many litter fragments occur, in the lower part hardly any, but here it is rich in bright quartz grains often covered with a net-work of black-brown hyphae just like the litter fragments. The leached sand layer under the H layer is ± 1 cm high and contains few humus particles.

The second type (II) adjoins the first in its occurrence and occupies $\frac{1}{3}$ part of the forest. It agrees more or less with the fibrous

mor-type and consists of an F layer which can be 8 cm thick, and a thin H layer. In the F layer numerous mycorrhizas and excrements are found. The latter occur in accumulations in places eaten away by animals and consist of grains of about 0.05 mm (mites) or of 1 mm (millipedes, fly larvae, earthworms etc.). Downwards the quantity of humus material increases among the litter fragments, so that the F layer gradually passes into the H layer which is at best 1 cm high and of a rather loose structure.

The third type (III) forms a transition from the fibrous to the granular type, and occupies the N.E. part of the forest. The F₁ layer is very thin or fails here. Downwards the litter is reduced to very small pieces surrounded by a good deal of humus material, so that an impression of a loose H layer is made though the litter particles are certainly the majority. The whole layer contains many roots and mycorrhizas but few excrements. The H layer is somewhat more compact and varies from 0.1 cm.

The utmost N.E. border of the forest has a thick F layer of a very loose structure, little fragmented. It is interwoven with many mould hyphae, and rests directly on the mineral underground.

Table 12. The pH in the different layers and in the different types of the floor in the beech forest 8 G.

Type of the floor	I	II	III	III	N. border
F ₀	5.3	5.1		5.3	5.3
F ₁	4.8	5.0	5.3	5.3	
F _x (-H)	4.4	4.0	4.3	4.5	
H	4.1	3.9			
H - A ₁	4.4	4.1	4.3	4.1	4.3
A ₁ (surface) . .	4.5	4.7	5.0	4.8	
A ₁ 40 cm. . . .				4.9	
A ₁ 60 cm. . . .				4.9	

In several places the pH of the floor was determined. A survey of the results is given in table 12. In spite of the diverse structure in the parts of the forest the pH does not show large deviations. Downwards the acidity increases from pH 4.3 in the F₀ layer to pH 4.0 in the humus layer. In the mineral underground the acidity is somewhat lower.

3. Some Climatological Factors

The climate of the Netherlands belongs to the damp moderate climates just as that of the greater part of Western Europe. The following data refer to a forty years' observation period (1901-1940) and are taken from communication 94a of the Royal Meteorological Institute at De Bilt (1950). The total average value of the precipitation is 715 mm. On an average most precipitation falls in the months of July, August and October (71-74 mm per month), the least in the months of February up to May inclusive (42-49 mm per month). For all that, precipitation is fairly regularly distributed over the year.

Winter is generally rather mild under the influence of the dominating S.W. and W. winds. The average number of days with snow does not amount to more than 17, the average temperature of the coldest month (January) is $+ 2.6^{\circ}$ C. Because of the same influence summer is rather cool (average temperature of the warmest month, July, 18.2° C). With E. winds, however, the weather is of a continental type, with sometimes long periods of frost in winter (min. -25° C), and high temperatures in summer (max. 38° C). Extremely high or low temperatures do, as a rule, not last very long. In the period of investigation, however, an extraordinarily severe winter (1946—1947) occurred, followed by a very hot summer (1947).

The climatological environmental factors in the litter layer of the experimental plot are in a high degree influenced by the forest, especially during the time that the beeches have leaves. The forest floor is sheltered against direct sunshine and the wind is checked. The temperature amplitudes are strongly decreased by it and the evaporation is diminished. The quantity and the distribution of the precipitation is also greatly influenced by the canopy. The degree of influencing is of course dependent on the density and the height of the foliage. The distribution of the precipitation over the surface is also influenced by stemflow. In consequence of this stemflow the litter layer is carried away from the ring around the stem foot, which is distinctly perceptible, especially with beeches. The degree in which the water contents may vary in the different layers of the floor appears from the values given in table A (appendix). The contents in volume percentages appear to vary for the different layers between the following extremes: F_0 : 0.1—26.3%; F_1 : 2.0—33.5%; F_x : 6.2—54.5%; H: 17.5—50.7%. From the downwards increasing minima of the water contents appears the great decrease of the desiccation in the lower layers; from the increasing maxima in the same direction appears the greater absorption power.

In order to characterize to some degree the fluctuations of the temperature in the floor, observations were made concerning the maximum and minimum temperature in the F and H layer in a place where these layers were each 2-3 cm high. Though these temperatures may vary dependent on the thickness of the litter layer, the values observed give an impression of the fluctuations of the temperature. Observations were made, with some interruptions, from June 1945 to July 1946. For four periods resp. autumn, winter, spring, and summer the course is shown in fig. 7.

At the same time observations in duplo were made concerning the relative value of the evaporation above the litter layer. Calibrated glass tubes closed with a round filtering paper were hung in a stand with the paper down so that the evaporating surface was about 5 cm above the litter surface. The quantity of the water evaporated was daily noted down, the average of the two observations, only differing little, is also shown in fig. 7.

For comparison the daily maximum and minimum temperatures

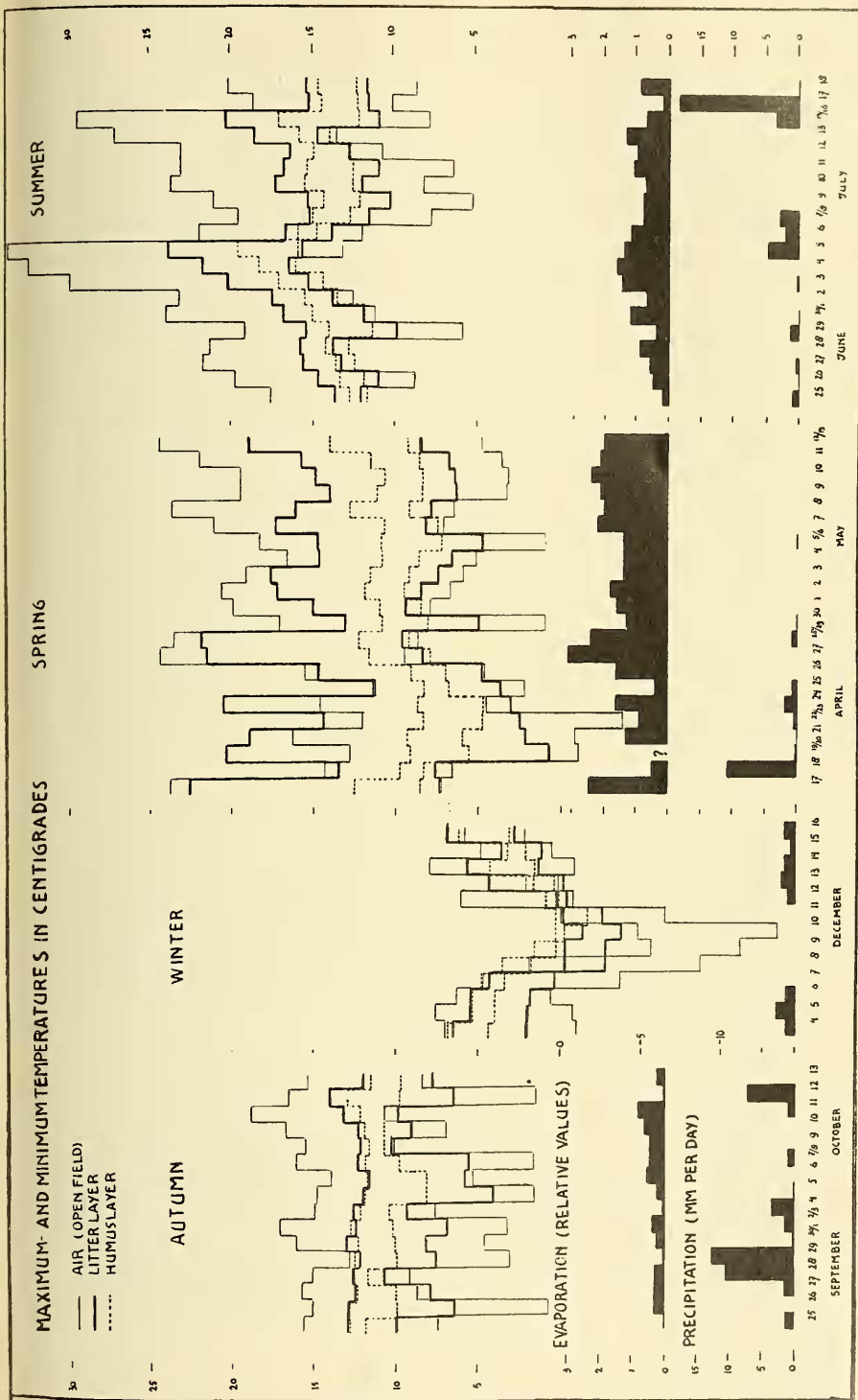


Fig. 7. Temperature, evaporation and precipitation during the year 1945—1946 in the beech forest 8 G.

and the precipitation in the open field are also shown in this figure. The former were measured in a meteorological station at about 2 m above the field surface. This observation station, where also precipitation was measured, was situated at a distance of a few hundred metres from the experimental area, so that without any objection the data can be compared with those of the experimental plot, resp. can be applied to it. The days on which during the periods mentioned no observations were made (in total 10) were omitted in the graph. The following day the maximum and minimum temperature of the two days' period were noted and the values of evaporation and precipitation were divided by two.

The graph shows how small in general the fluctuations of temperature in the soil floor are, compared with those in the open field. Only in spring when the trees have no leaves yet, the maxima in the layer reach about the same values as those in the open field, may even exceed them. After the leaves have budded (about the 1st May in 1946) the maxima in the F layer remain considerably lower than those in the open field. The fluctuations in the H layer are of course much smaller than those in the F layer. In autumn and winter the average temperature (taken from the averages of minimum and maximum temperature) in the H layer is higher than that in the F layer; in the short but severe frost period in December the difference was even very considerable. In spring and summer the average temperature in the H layer is lower than that in the F layer. That the temperature may also rise considerably in the H layer appears from the observation of the 5th July 1946: with an air temperature of 34° C, a temperature of 19.4° C was reached in it.

The relative evaporation values are highest in spring. This is caused by the high temperature of the air above the litter and by the smaller shelter against wind in consequence of the bareness of the trees. A comparison of the evaporation values of a week at the end of April with those of a week in the beginning of July shows the second being 59% of the first, whereas in the open field the evaporation in July was 76% of that in April. Accordingly the litter layer is exposed to a greater desiccation in spring than in summer, though the temperatures in the litter layer are considerably higher in summer.

CHAPTER V

THE ANIMAL COMMUNITY IN THE FLOOR

As explained in chapter III the composition of the soil fauna is investigated for methodical and practical reasons in four different ways complementing each other. By each way of investigation a separate part of the fauna is obtained, which we will discuss here successively. For the sake of brevity we will use the following names for these parts of the fauna:

Mesofauna : A. Microarthropods : mites and collembolae of 0.1—2.0 mm length, obtained by desiccating samples of 40 cm³.

- B. Remaining mesofauna : nematodes, rotifers, tardigrads obtained by plunging samples of the same size.

Macrofauna : C. Hemiedaphic macrofauna : worms, slugs and macroarthropods obtained by desiccating samples of 4 dm³.

- D. Epedaphic macrofauna : macroarthropods obtained by the trap technique.

A. MICROARTHROPODS

Mites (Acari) and smaller collemboles (varying in size from 0.1—2.0 mm), belong to this group. The order of Acari (as far as present in our forest soils) is divided into the suborders Parasitiformes, Trombidiformes and Sarcoptiformes.

Of the Parasitiformes the Gamasides and Uropodina are important. In the periodic catches neither they nor the Trombidiformes were further identified, with the exception of some important families. Of the Sarcoptiformes the Acaridae are also chiefly taken as a group. The Oribatei, however, being the most important of all mites living in the soil, were identified to species as far as possible. Sometimes this led to difficulties especially with immature animals, which were then mostly taken together in groups.

Of the smaller collemboles principally the Poduromorpha are important. Only some species that can be recognized without microscopical observation of details, are mentioned separately. The others are taken as a group.

Some remarks on reproduction and development of microarthropods may be made here.

About all microarthropods reproduce by means of eggs, which the different species lay in diverging numbers. From literature the following is known :

Oribatei and Parasitiformes generally lay one or two eggs at the same time. This recurs, however, several times so that the total number of eggs per female may be very considerable. Parthenogenesis occurs in several families (GRANDJEAN 1948). In Trombidiformes and Acaridae eggs are often produced in large numbers. Parthenogenesis is well known here.

Collembola mostly lay their eggs in groups of 8-12, *Hypogastrura manubrialis* Tullbg. even up to 35 pieces (RIPPER 1930). In these animals deposition of the eggs also recurs frequently with intervals of some weeks.

In all Acari a larva with three pairs of legs develops from the egg. Originally further development gives successively three nymph stages with four pairs of legs, proto-, deuto- and trito-nympha, the latter developing into the adult. Of the mites concerned in this study only the Oribatei have this original way of development. The Parasitiformes only possess two nymph stages, proto- and deuto-nympha. The latter often moves by clinging to other animals (phoresy). The greater part of the Acaridae has only a proto- and trito-nympha. In several free living Acaridae an intermediate stage with a very aberrant shape occurs between the two nymph stages, the so called heteromorphous deuto-nympha or hypopoda, often also dispersing by phoresy. In Trombidiformes generally only one nymph stage, the deuto-nympha is left.

The development of the Collembola takes place without important morphological changes. The adult stage is reached after a number of moultings. Also after reaching maturity moulting is continued.

Successively the vertical dispersal¹⁾, the horizontal dispersal and

¹⁾ Dispersal is always used here in the sense of state of being dispersed.

the seasonal fluctuations of these microarthropods will be discussed in the general part. In the special part of each species or larger unit the data found and data from literature will be summarized.

a. General Part

1. Vertical Dispersal

The investigation of the vertical dispersal of the microarthropods during the course of the year began in May 1944 in the S. W. part of the beech forest 8 G where the separate layers in the litter were clearly distinguished and ended in March 1946. In consequence of the war these investigations were interrupted from August 1944 till August 1945, when they were resumed and extended over the whole plot of 85 years' old beeches. From the separate layers of the litter profile (mostly 4) samples were taken vertically below each other, which together will be called a set. On a date of investigation mostly 3 sets of samples were taken, which together will be called a series. The series of samples were taken about every two months. In each of the months May and July 2 series of 3 sets were taken, the second series of which was taken a week after the first with a view to the available apparatus. A week's lapse of time is no objection to regarding them as one double series. All other series consisted of three sets. The series of May, July and August 1944 are all from the S.W. part of the forest. Of the other series one always came from the S.W. part of the forest, the two others from various places in the forest with a regularly developed litter profile.

The results of the counts are summarized in table A (appendix). Only those species and groups are taken into account that appeared in such density and frequency that they were regularly found in the samples.

If possible the young and adult specimens were distinguished. In each column the first number indicates the number of young animals, the second that of the adults. If this distinction was not possible the total number was placed in the middle of the column. The air-dry weights of all samples and the water contents calculated from them and expressed in volume percentages have been given. This is preferable to expressing the water contents in percentages of the dry weight, because the specific weight of the material in the litter profile highly increases downwards, in consequence of a more compact composition and the presence of mineral substance owing to which the water contents of the different layers expressed in percentages of the weight, are not mutually comparable. The volume of the samples was 40 cm³; only in the case of the F₀ samples of 1944 volumes of ± 1000 cm³ (May and July) and of 200 cm³ (August) were taken. As well determining the volumes of the samples of 1000 cm³ as counting the animals were done less exactly than with the samples of 40 cm³. For this reason the number of animals is indicated by symbols in these samples to prevent confusion with the other data. Except for two cases the four different layers of litter (F₀, F₁, F_x and H) are found in all sets of samples. The F₁ layer is lacking in the first set of May since it was badly developed in that place. In the October series in all sets the separate F₀ and F₁ samples were substituted by a F₀—F₁ sample, as it was then impossible to separate the two layers well. In frosty weather (December and January series) the samples were cut from the frozen layers and afterwards measured in the normal way. From the dry weights it is clear that the samples thus became too small. This, however,

hardly affects the figures on the vertical dispersal. To some sets a sample of the A_1 layer was added. The examination of these samples only yielded such small quantities of animals, that this layer needs no further consideration.

The summarizing table already shows several facts. Firstly most species appear to have a high frequency percentage, i.e. the species mentioned here occur, even if they have a small density, in all or nearly all samples, or in the samples of certain layers. This proves that the sample is sufficiently large to express the characteristic composition of the predominating species of the microarthropod fauna. For species with a very small density considerably larger samples ought to have been taken. That this leads to practical difficulties, was already explained in discussing the technique. A second fact that strikes the eye in considering the table is the irregularity in density of many species. Side by side with local concentration local scarcity occurs. These differences are difficult to explain. It seems most probable to me, that there are differences in the possibility of finding food and in other ecological conditions.

Also the vertical dispersal of the different species is already fairly clear from the summarizing table. It becomes even clearer if we calculate the average of each species from the data of the samples of one layer of a series. In consequence of the small number of parallel sets of each series it is not allowed to deduce from them fluctuations in the population density during the course of the year, the less so since the investigations do not refer to an uninterrupted period of time. To compare the density in the different layers, which diverge much more, the calculated averages are illustrative, though it should be remembered that here too, in consequence of the small quantity of parallel sets, real significance may only be attached to relatively large differences. Table 13 gives the averages of the most important species in the different layers. In all species the vertical dispersal in the series of August 1944, December 1945 and January 1946 shows an important deviation from that in the other series. Drought (August) and frost (December and January) are the causes of these deviations, and will be discussed lower down.

To get a survey of the vertical dispersal of the different species in "normal" circumstances, based on investigations during the whole year, a general average was calculated for each species from the averages of the series, exclusive of those of August 1944, December 1945 and January 1946.

The averages of F_0 are calculated from two averages of the series only, viz. those of August 1945 and March 1946, since the values of May and July fell out (quantities estimated), the values of F_0 — F_1 of October are considered to belong to F_1 because of the condition of the litter and finally, as mentioned above, the averages of August 1944, December and January were not considered because of the abnormal dispersal. Therefore the averages of F_0 do not refer to the population of this layer after the falling of the leaves till March and they are certainly less reliable than

Table 13. Averages of the weights and the water contents of the samples and the densities per 40 cm³ of the different species in the different layers on the successive sampling dates and total averages calculated from these, exclusive of abnormal circumstances (Aug. 1944, Dec. 1945, Jan. 1946)¹⁾.

		May '44	July '44	Aug. '44	Aug. '45	Oct. '45	Dec. '45	Jan. '46	Mrch '46	total average
Weights of the samples, air-dry in g	F ₀			(11.4)	4.3		2.5	2.5	3.5	3.9
	F ₁	4.2	3.7	3.5	3.9	3.9	2.3	2.2	3.7	3.8
	F _x	4.8	4.4	5.0	4.7	5.2	4.2	3.4	4.6	4.8
	H	10.2	10.4	9.8	9.7	10.6	10.4	8.8	8.2	9.8
Water con- tents in vol.%	F ₀			(0.8)	23.6		(14.0)		11.4	17.5
	F ₁	6.4	14.2	2.2	27.5	20.0	(19.6)	(19.3)	26.3	18.9
	F _x	13.9	19.5	7.1	29.3	41.6	(28.1)	(26.9)	35.8	28.0
	H	30.9	40.7	19.3	43.8	37.9	37.6	38.4	42.3	39.1
<i>Nanherman- nia elegantula</i>	F ₀			(—)	1.3		—	—	—	0.7
	F ₁	—	0.3	—	1.0	—	—	—	1.3	0.5
	F _x	2.7	3.5	0.3	2.0	6.0	0.3	0.3	3.7	3.6
	H	0.3	0.7	—	0.3	1.0	—	0.3	0.7	0.6
<i>Hypochtho- nius rufulus</i> juv.	F ₀			(—)	6.7		—	—	1.3	4.0
	F ₁	18.8	16.3	—	7.7	9.0	—	0.3	2.3	10.8
	F _x	27.2	4.3	5.3	9.7	7.0	2.0	6.0	11.3	11.9
	H	6.7	1.7	5.3	4.0	1.7	3.0	3.3	3.3	3.5
<i>Hypochtho- nius rufulus</i> ad.	F ₀			(—)	2.3		—	—	0.3	1.3
	F ₁	4.2	1.5	0.3	3.3	4.0	—	—	2.7	3.1
	F _x	3.0	0.7	4.7	1.0	2.3	—	1.0	1.7	1.7
	H	0.5	0.3	0.7	0.7	—	0.3	2.0	1.0	0.5
<i>Brachych- thonius</i> sp.	F ₀			(—)	—		—	—	1.3	0.7
	F ₁	0.8	3.3	0.7	2.3	—	1.3	—	6.0	2.5
	F _x	12.0	9.0	3.7	24.0	9.0	10.3	1.0	8.0	12.4
	H	5.7	2.8	2.7	6.0	6.3	0.3	0.3	0.3	4.8
<i>Nothrus</i> <i>silvestris</i> juv.	F ₀			(—)	8.0		—	—	6.7	7.4
	F ₁	7.6	0.6	0.6	8.3	9.3	2.0	0.3	6.7	6.5
	F _x	54.6	27.5	67.3	134.3	161.0	88.3	53.0	40.7	83.6
	H	41.5	12.8	28.0	37.3	59.7	41.3	43.3	36.7	37.6
<i>Nothrus</i> <i>silvestris</i> ad.	F ₀			(—)	1.0		—	—	2.3	1.7
	F ₁	2.6	4.3	—	8.0	10.3	2.3	—	14.6	8.0
	F _x	12.1	11.3	8.1	25.6	38.6	13.6	16.3	34.3	24.4
	H	3.0	0.8	2.3	6.6	6.0	4.6	5.0	2.6	3.8
<i>Platynothrus</i> <i>peltifer</i> juv.	F ₀			(—)	—		3.0	24.7	10.3	5.2
	F ₁	3.4	1.0	—	—	4.7	2.0	3.0	6.3	3.1
	F _x	1.7	0.3	—	0.3	—	0.3	—	0.3	0.5
	H	1.3	—	—	—	—	—	—	—	0.3

¹⁾ The F₀ averages of August 1944 are parenthesized because these values refer to a larger volume (± 200 cm³). Water contents of F₀, F₁ and F_x samples of December and January refer to frozen samples.

table 13 (continued)

		May '44	July '44	Aug. '44	Aug. '45	Oct. '45	Dec. '45	Jan. '46	Mrch '46	total average
<i>Platynothrus peltifer</i> ad.	F ₀			(0.1)	4.7		—	—	0.3	2.5
	F ₁	2.6	0.7	1.0	1.0	1.7	0.7	1.7	5.3	2.3
	F _x	1.8	0.7	0.7	—	0.7	—	—	1.0	0.8
	H	0.2	—	—	—	—	—	—	—	0.0
<i>Oppia neerlandica</i> a.o. <i>Eremaeidae</i>	F ₀			(0.1)	8.3		—	—	1.3	4.7
	F ₁	49.6	105.7	2.7	35.0	24.3	8.7	13.7	16.3	46.2
	F _x	153.7	191.2	136.3	151.7	171.7	182.3	106.0	128.0	159.3
	H	96.7	32.5	56.3	40.3	140.3	84.3	96.0	69.0	75.8
<i>Tectocephus velatus</i> juv.	F ₀			(—)	0.7		—	—	0.7	0.7
	F ₁	15.2	6.5	1.0	1.7	6.3	—	0.7	1.0	6.1
	F _x	8.0	6.3	11.3	1.3	23.0	1.7	9.0	1.0	7.9
	H	2.7	0.2	—	—	3.3	—	—	—	1.2
<i>Tectocephus velatus</i> ad.	F ₀			(—)	0.7		—	—	0.3	0.5
	F ₁	21.6	8.7	1.0	1.7	25.0	—	2.7	0.7	11.5
	F _x	7.8	5.0	8.7	1.0	22.3	1.3	3.0	—	7.2
	H	1.2	0.2	0.7	—	1.0	—	—	—	0.5
<i>Oribatula tibialis</i> ad.	F ₀			(0.1)	0.7		—	0.3	2.3	1.5
	F ₁	0.6	1.0	0.3	1.3	6.7	3.3	1.7	—	2.0
	F _x	0.2	—	—	—	1.3	1.0	0.7	—	0.3
	H									
<i>Chamobates schützi</i> ad.	F ₀			(0.1)	7.3		—	—	1.3	4.3
	F ₁	7.0	6.3	5.0	1.0	7.3	5.0	3.3	2.0	4.7
	F _x	1.2	2.0	4.3	—	1.0	—	0.3	0.3	0.9
	H	0.3	0.2	0.3	—	—	0.3	—	—	0.1
<i>Phthiracarus borealis</i> ad.	F ₀			(—)	0.7		—	—	0.3	0.5
	F ₁	2.2	2.0	0.7	—	0.3	0.3	—	0.7	1.4
	F _x	5.2	2.0	0.7	0.7	3.0	1.7	1.0	1.3	2.4
	H	0.5	0.2	—	—	0.3	—	—	—	0.2
<i>Oribotritia loricata</i> juv.	F ₀			(—)	—		—	—	—	—
	F ₁	—	—	—	—	—	—	—	—	—
	F _x	2.2	0.3	0.3	—	—	2.0	—	3.0	1.1
	H	2.7	1.7	1.0	—	1.0	—	1.0	3.0	1.6
<i>Oribotritia loricata</i> ad.	F ₀			(—)	—		—	—	—	—
	F ₁	1.2	2.0	—	0.3	0.3	—	—	0.7	1.3
	F _x	8.2	5.2	1.0	2.7	3.3	4.0	2.7	8.0	5.5
	H	2.7	1.7	0.7	0.7	3.3	2.3	2.0	4.0	2.5
<i>Pseudotritia minima</i>	F ₀			(—)	—		—	—	—	—
	F ₁	—	1.2	—	—	1.0	—	—	—	0.4
	F _x	2.7	4.2	1.0	0.7	5.0	3.0	1.7	0.7	2.6
	H	27.0	32.8	8.3	9.3	45.0	16.3	9.3	22.7	27.4

table 13 (continued)

		May '44	July '44	Aug. '44	Aug. '45	Oct. '45	Dec. '45	Jan. '46	Mrch '46	total average
<i>Acaridae</i> juv.	F ₀			(0.1)	2.3		0.3	—	5.0	3.7
	F ₁	1.2	6.2	0.3	3.7	25.0	12.7	9.7	7.7	8.8
	F _x	6.0	4.8	0.3	1.3	17.7	5.3	2.7	14.3	8.8
	H	7.3	0.7	1.7	1.0	1.0	1.3	0.7	0.7	2.1
<i>Trombidi-</i> <i>formes</i>	F ₀			(5.5)	14.3		1.3	1.0	4.0	9.2
	F ₁	57.2	66.0	27.0	26.0	25.0	7.7	14.0	5.3	35.9
	F _x	70.2	48.8	46.7	37.3	34.0	23.0	25.0	25.3	43.1
	H	41.3	17.8	23.0	19.3	29.0	16.0	18.7	11.3	23.7
<i>Parasitidae</i>	F ₀			(0.1)	2.7		—	—	8.0	5.4
	F ₁	4.4	9.0	1.3	6.0	9.0	2.3	1.0	5.7	6.8
	F _x	6.7	8.5	8.7	6.7	9.0	5.0	2.7	5.3	7.2
	H	3.3	2.8	3.7	1.7	6.0	3.7	4.7	3.0	3.4
<i>Cilliba</i> sp.	F ₀			(—)	—		—	—	5.3	2.7
	F ₁	2.2	1.3	—	5.3	7.0	0.3	—	31.7	9.5
	F _x	6.5	5.7	6.0	19.0	15.3	3.7	0.3	10.7	11.4
	H	3.7	5.2	1.3	10.7	2.7	12.3	9.0	5.0	5.5
<i>Trachytes</i> sp.	F ₀			(—)	7.3		—	—	3.3	5.3
	F ₁	1.8	5.4	1.7	7.0	5.3	1.3	0.3	12.3	6.4
	F _x	2.3	2.5	3.0	1.7	1.7	2.3	2.0	3.0	2.2
	H	—	0.7	—	0.7	—	—	—	0.3	0.3
<i>Isotoma minor</i>	F ₀			(—)	6.0		—	—	1.0	3.5
	F ₁	1.4	6.7	—	33.7	7.3	—	—	7.0	11.2
	F _x	1.5	11.8	3.0	24.7	24.0	3.0	5.0	16.7	15.7
	H	0.2	0.8	0.7	0.7	5.0	6.3	15.7	5.3	2.4
<i>Isotoma</i> sp.	F ₀			(0.2)	3.7		—	—	2.0	2.9
	F ₁	2.6	13.2	0.3	4.3	5.3	—	0.3	2.0	5.5
	F _x	3.2	9.3	5.7	6.3	8.0	2.7	3.3	0.3	5.4
	H	0.8	1.0	1.0	1.0	—	—	—	—	0.6
<i>Poduromor-</i> <i>pha</i>	F ₀			(0.2)	6.0		—	—	0.3	3.2
	F ₁	5.4	11.3	1.3	10.3	3.7	0.3	2.3	2.0	6.5
	F _x	25.8	64.3	30.3	78.0	17.3	19.0	6.7	22.0	41.5
	H	53.2	36.2	13.3	32.7	40.0	36.3	35.0	42.7	41.0
<i>Hypogas-</i> <i>trura armata</i>	F ₀			(22.1)	26.7		—	—	2.3	14.5
	F ₁	36.0	42.7	51.3	13.7	20.3	10.7	28.7	10.0	24.5
	F _x	6.7	10.3	7.3	—	16.0	12.3	6.0	3.3	7.3
	H	0.8	1.3	—	—	12.0	0.3	4.3	0.7	3.0
<i>Onychiurus</i> <i>armatus</i>	F ₀			(—)	—		—	—	—	—
	F ₁	0.6	2.5	—	0.7	1.7	—	—	8.0	2.7
	F _x	1.8	7.8	3.0	5.0	11.0	3.0	2.0	8.7	6.9
	H	1.3	2.2	0.7	2.0	5.0	2.0	4.3	5.7	3.2

VERTICAL DISTRIBUTION OF MICROARTHROPODS IN BEECH FOREST FLOOR

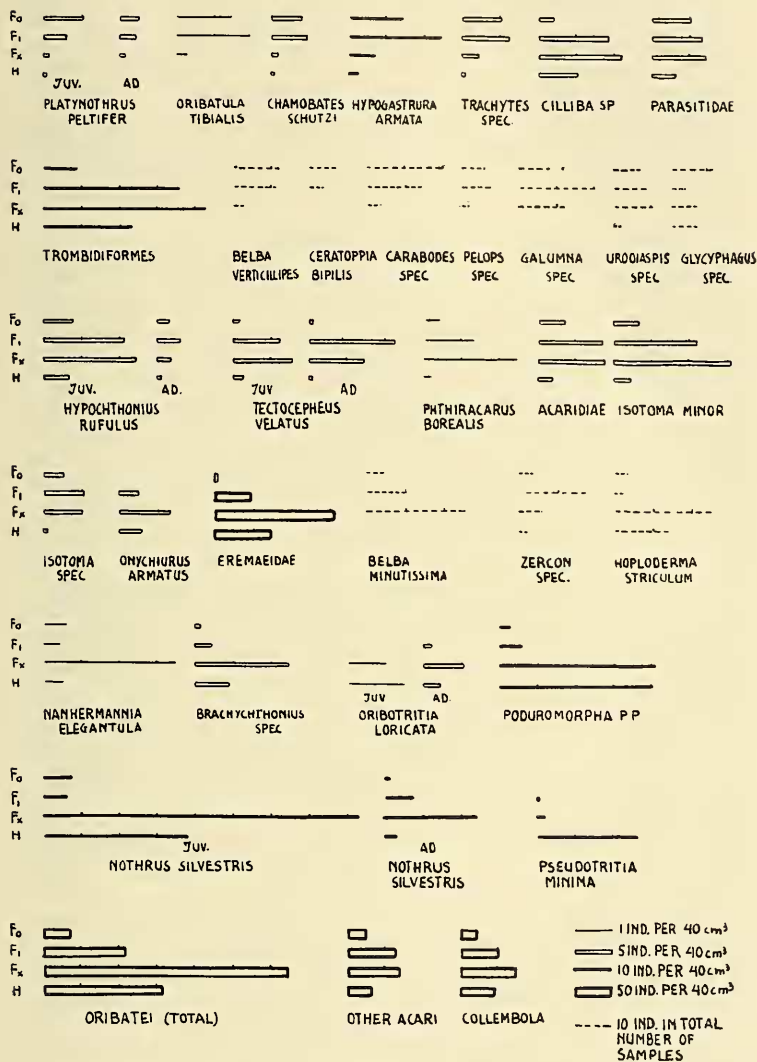


Fig. 8. Vertical dispersal of the microarthropods in the floor of the beech forest 8 G.

the averages of the other layers, in consequence of the smaller number of observations they are based on. As they gave together, with the latter, a logical figure of the dispersal they were inserted in table 13 after all.

Fig. 8 gives a graph of the average densities. The greatly varying densities in which the different species occur made it

necessary to use three scales in order to get a clear idea of all species.

Of species with a small density all individuals which were caught in each layer during the whole year, were added together. Their numbers are presented in fig. 8 by broken lines. Though the quantities are small and the influence of chance is great the diagrams do give an impression of the vertical dispersal. Since part of the F_0 samples was estimated the length of the lines indicating the density in this layer are also estimated at their most probable size.

From the diagrams it appears that there are species which distinctly prefer a certain layer, of which *Pseudotritia minima* is the most illustrative. Next there are species that are less specific and have their greatest density in two or even three adjoining layers. No preference could be stated in the cases of Gamasides (Parasitidae for the greater part) and Trombidiformes.

For a causal explanation of the vertical dispersal a great deal more must be known of the life habits of the different species of the microarthropods. We can only offer some suggestions.

From the graph of all Oribatei it appears, that the F_x layer is most densely populated. The greater part of the Oribatei feed on dead leaves and moulds. It is clear that this layer offers the best conditions of sustenance, since the litter has already been broken down into small parts and there are many mould hyphae present.

Some species have their optimum in the F_0 and F_1 layer. These are chiefly rather big species such as *Platynothrus peltifer*, *Belba verticillipes*, *Ceratoppia bipilis* and *Carabodes* sp. But also smaller species, such as *Oribatula tibialis* and *Chamobates schützi* prefer these layers. Probably these animals do not feed on litter, but on mould and algae that occur in the youngest litter material. It is possible that some of these species are only subferent inhabitants of the litter layer and have their optimum in the other merotopes e.g. in the rind of tree-trunks. Anyhow, they are adapted to the more extreme environmental circumstances in the upper layers of litter, which is affirmed by the lack of vertical emigration at times of drought (see lower down).

Of the species of which juvenile and adult animals were separately counted the former appear to have their optimum deeper than the latter: *Hypochthonius rufulus*, *Nothrus silvestris*, *Tectocephus velatus* and *Oribotritia loricata*. Perhaps the more equable conditions of moisture and temperature are more appropriate to the delicate larva and nymph stages, though it is not excluded that egg deposition and/or feeding questions play a part also. An exception is *Platynothrus peltifer*, the juvenile specimens of which have their optimum in the F_0 layer just like the adults.

Remarkable is the difference in dispersal between the small Poduromorpha and *Hypogastrura armata*, also belonging to this group. The adaptation to their environment that these groups show will be discussed in the special part.

Trombidiformes and Parasitidae, both groups with chiefly

carnivorous feeding habits, are met with in all layers, though in these groups too a preference for certain layers may seem to exist if they are divided into species.

The influence of drought on the vertical dispersal may be studied by comparing dispersal in August 1944 and that in the preceding months, all samples taken from the same place in the forest (see table 13).

The long drought of August 1944, when during 18 days preceding the date of sampling practically no rain fell and the temperature was rather high (lowest maximal temperature of the preceding fortnight 28°C), was the cause of desiccation especially of the upper layers of litter (see water content table 13). It seems that the greater part of the microarthropods retired into lower layers. Examination of some samples of sand immediately under the layer of litter showed that they did not penetrate into the sand layer. So an increase of density in the lower layers must take place. This increase will be clearest in those species that have their maximal density in the upper layers, and if these layers are not too thin in comparison with the lower, less desiccated layers. As the lower layers are thicker than the upper layers in this case, the increase of density in the former will be less striking than the decrease in the latter.

Platynocheilus peltifer, *Oribatula tibialis*, *Chamobates schützi* and *Hypogastrura armata* belong to the species with an optimum in the F_0 and F_1 (fig. 8). These very species appear to be less sensible to desiccation and are most numerous in the desiccated layers of litter. With this degree of desiccation they do not withdraw downwards and cause no increase of density there. However, *Trachytes* sp., with the same dispersal, decreases in the upper layer but does not show a distinct increase in F_x and H.

Trombidiformes and Parasitidae, which occur in all layers of forest soil, remain in small density in the upper layers during the period of drought. No increase of density in the lower layers can be stated.

Of the species that have their optimum in F_1 and F_x *Hypochothonius rufulus* and *Tectocepheus velatus* show lower densities in F_0 and F_1 and higher densities in F_x and H than in normal circumstances. *Cilliba* disappears from the upper layers, but an increase in the lower layers is not demonstrable. *Phthiracarus borealis*, Acaridae deuto-nymphae, *Isotoma minor* and *Onychiurus armatus* even decrease in the lower layers too. Perhaps this decrease may be ascribed to mortality. In a species like *Phthiracarus borealis*, which can contract to a ball, the possibility exists that it is able to survive the period of drought in a state of torpidity and it is not caught in desiccating these samples. In recatching experiments (p. 33), however, there was no indication of such a state of torpidity.

Oppia neerlandica and other Eremaeidae, which are normally very numerous both in F_1 and F_x , withdrew almost wholly from the F_1 layer and showed a small decrease in the F_x layer.

Nothrus silvestris is in quantitative respect by far the most important of the species that have their maximum in F_x or in F_x and H. Both adult and juvenile animals only occur in small numbers in the upper layers. In dry weather they withdraw wholly or almost wholly from these layers. As is to be expected this does not cause an increase in the lower layers. The high density of young animals in F_x and H is probably to be attributed to birth (see p. 84, fig. 11). The adult animals, which fluctuate less, also partially retire from the F_x layer and cause an increase in H.

The decrease of *Nanhermannia elegantula* and *Brachychthonius* sp. also in the lower layers is probably again to be attributed to mortality like that of the small collembolae that are summarized as Poduromorpha. Perhaps the decrease in catching *Oribotritia loricata* and *Pseudotritia minima* may be attributed to a state of torpidity caused by drought just like in the case of *Phthiracarus borealis*.

To summarize we can say that desiccation of the litter layer has a different effect on different microarthropod species. On the species that are adapted to the most extreme environmental conditions the desiccation has little influence either on their quantity or on their vertical dispersion.

The other species — as far as they normally occur in the upper layers — withdraw from these layers. In some cases an increase of the density in the lower layers is to be inferred. In other cases the density of the species decrease in all layers of litter. This is probably to be attributed to mortality in consequence of drought. In Phthiracaridae this may be a consequence of a state of torpidity.

In consequence of the interruption of the sampling in August 1944 it was not possible to get the supposed mortality proved by a lower density after the period of drought.

The effect of frost on the vertical dispersal may be seen in the series of December 1945 and January 1946, two days of severe frost preceding the date of sampling in December, 12 days of frost that of January. On both dates the litter was frozen down to the humus layer.

The influence of frost cannot be traced in the same way as the influence of drought by comparing the densities in the series concerned and those in the series of the preceding months. From August 1945 the samples were taken spread over the whole forest, in consequence of which the averages of the series mutually show greater differences. Moreover, the frozen samples turned out too small as was already said. Because of these reasons the averages can hardly be compared with those of October 1945 and March 1946 and they have to be considered by themselves in regard to the vertical dispersion of the species in "normal" circumstances (table 13).

The relatively small quantities in the F_0 samples may partially be a consequence of the fact that this layer of new litter is not yet populated by microarthropods and partially of the withdrawal of

the animals into the lower layers. Now *Platynothrus* too proves to be adapted to extreme circumstances: the young animals keep their maximum in the F_0 , the adult animals in the F_1 . *Oribatula*, *Chamobates* and *Hypogastrura* occur hardly or not at all in F_0 (have probably not yet penetrated into it in autumn), but keep their maximum in F_1 . Neither *Trachytes* nor the Parasitidae and Trombidiformes show a downward migration. *Hypochthonius*, *Tectocephus*, *Cilliba* and *Isotoma* do: the F_1 layer is wholly left by *Hypochthonius* and *Isotoma minor*, the other species have a much lower density here than in normal circumstances. *Cilliba* and *Isotoma minor* have chiefly retired to the H layer. In Acaridiae deutonymphae and *Phthiracarus* on the contrary we find no vestige of withdrawal. All other species have retired from the upper layers. *Pseudotritia* having its optimum in H, retains its normal dispersal.

Though the series averages of March 1946 and October 1945 are not quite comparable because of the local differences in density, none of the densities of the species in March appears to be considerably lower than those of October so that a great mortality caused by the frost is not probable. However, the frost was not very severe nor did it last long that winter. The results of the investigations during and after the very severe winter of 1946—1947 also point to the same conclusion (see p. 80), so that it seems justified to say that the fauna of microarthropods does not suffer seriously from frost.

2. Horizontal Dispersal

The data from which the vertical dispersal was deduced, refer to samples that were exclusively taken from places where the layer of litter had regularly developed and that were not regularly spread through the forest. For this reason they cannot be used to get an exact idea of the dispersal of the species over the whole forest floor. However, one important fact came to light: it appeared that the species with the greatest density occurred in all or nearly all samples.

To get a complete idea of the dispersal of all species it would have been necessary to analyse a great number of samples from all layers, on short distances, regularly spread over the experimental plot and taken in the shortest time possible under rather constant weather conditions. To get an exact idea of the dispersal of those species that have a small density, moreover, it would have been necessary to take samples bigger than 40 cm³.

The results of such an investigation into the homogeneity of the dispersion, no doubt, would have been of importance. However, such detailed examination of the horizontal dispersal was not intended here and the examination was confined to two series of 15 samples regularly spread over the 85 years' old part of the stand to get to know if all species occur in all parts of this forest. All samples were taken from the most densely populated F_x layer. The first series was taken in the early spring of 1944, the second series in the autumn of 1947. In the latter case from each of the

three floor-types, I, II and III (see p. 54, fig. 5), 5 samples distributed over each of the parts were taken.

The frequency percentages that give the number of samples in which a species occurs in percentages of the whole number of samples, are shown in table 14. In this table are also given the average densities of the species in the samples of 1944 and in those of the three floor-types of 1947.

The average densities in the different types are based on too few data to be able to calculate statistical differences, the more so as the data vary much. They only serve to show that the densities

Table 14, Horizontal dispersal of the microarthropods in the F_x layer of the beech forest 8 G expressed in frequency percentages and in average densities in the three parts of the plot (I, II, III) with different floor type.

	Frequency percentage (of a total of 15 samples)		Average density in numbers per 40 cm ³			
	Spring '44	Autumn '47	Spring '44	Autumn '47		
				I	II	III
<i>Nothrus silvestris</i> .	100	100	113.2	114.3	98.9	78.5
<i>Oppia neerlandica</i> .	100	100	176.7	44.0	160.5	91.8
<i>Eremaeidae</i> div. .	100	100		21.2	23.5	30.8
<i>Hypochthonius</i>						
<i>rufulus</i>	100	93	23.3	17.5	13.8	4.5
<i>Trombidiformes</i> . .	100	100	32.4	42.3	23.8	40.8
<i>Poduromorpha</i> . .	100	100	53.1	45.8	43.8	47.0
<i>Parasitidae</i> . . .	100	100	9.8	5.5	6.3	3.3
<i>Brachychthonius</i> sp.	93	96	27.4	4.3	2.5	5.3
<i>Cilliba</i> sp. . . .	100	80	8.5	2.8	7.5	2.5
<i>Oribotritia loricata</i>	87	87	4.4	5.0	5.5	2.3
<i>Isotoma minor</i> . .	87	40	17.7	1.3	0.3	2.5
<i>Trachytes</i> sp. . .	87	13	6.3	0.5	—	0.3
<i>Hypogastrura</i>						
<i>armata</i>	73	27	4.1	0.3	—	0.8
<i>Pseudotritia minima</i>	33	93	2.8	93.3	30.3	5.8
<i>Onychiurus armatus</i>	40	80	2.8	1.5	2.8	11.0
<i>Hoploderma</i>						
<i>striculum</i>	27	60	0.7	3.3	3.8	0.3
<i>Tectocephus</i>						
<i>velatus</i>	73	67	15.3	6.0	2.8	1.0
<i>Nanhermannia</i>						
<i>elegantula</i> . . .	53	73	10.2	4.0	0.8	0.8
<i>Phthiracarus</i>						
<i>borealis</i>	40	53	0.7	4.0	4.0	0.3
<i>Platynothrus</i>						
<i>peltifer</i>	40	33	0.4	3.3	—	0.3
<i>Belba minutissima</i> .	27	47	0.6	—	1.5	3.0
<i>Chamobates schützi</i>	47	20	2.1	0.3	—	—
<i>Urodiaspis tecta</i> .	27	13	0.7	0.3	0.3	—
<i>Pelops aurita</i> . .	27	7	0.4	—	0.3	—
<i>Cosmochthonius</i>						
<i>lanatus</i>	20	7	0.3	—	—	0.3
<i>Oribatula tibialis</i>	13	7	0.4	0.3	—	—
<i>Galumna</i> cf. <i>dorsalis</i>	—	13	—	—	—	0.8
<i>Belba verticillipes</i> .	33	—	0.3	—	—	—
<i>Folsomia</i>						
<i>quadrioculata</i> . .	20	—	0.5	—	—	—

in the F_x layer in the three types generally lie in the same order of magnitude and thus the species are rather equally distributed. An exception is *Pseudotritia minima*, the high averages of which in type I and II are caused by the large numbers of individuals in one of the samples of each type. For species with a high density, the equal distribution appears also from the high frequency percentages. In fig. 9 the frequencies of all species (larger groups are omitted) are plotted against the average densities of these species. All species that have a density greater than 10 per 40 cm³ occur with a frequency of 87—100% i.e. in at least 13 of the 15 samples. Exceptions are only *Tectocephus velatus* and *Nanhermannia elegantula*, which show local concentrations causing high averages, though

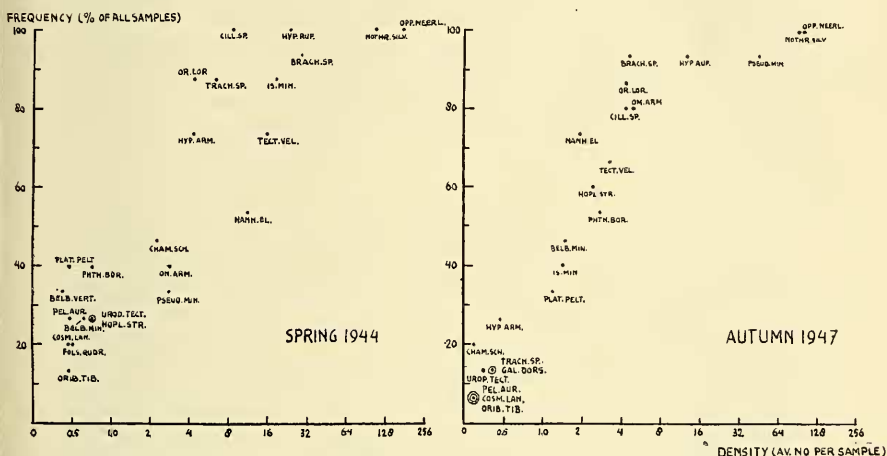


Fig. 9. Frequency - density relation of microarthropod species in the F_x layer of the beech forest 8 G. In each case data refer to 15 samples of 40 cm³.

the frequency percentage is lower than 87. Some species have a high frequency percentage in spite of their small density: *Cilliba* sp., *Oribotritia loricata*, *Trachytes* sp. and *Brachychthonius* sp. In general, however, we find a lower frequency percentage in species with a small density.

In increasing the number of the samples the frequency percentages would have had a higher reliability. In a series of 15 samples the exactness of the frequency percentages is only $6\frac{2}{3}\%$. Nevertheless it is excluded that an increase of the number of samples would have given considerably different results. The frequency percentages of 1944 and 1947, in general, agree rather well. If this is not the case it may be attributed to a difference in density of the species concerned at the time of sampling. They may be a consequence of seasonal differences but also of annual fluctuations in the density.

Remarkable differences in density and frequency show *Isotoma minor*, *Trachytes* sp. and *Hypogastrura armata*, which were more

numerous and frequent in 1944 and *Pseudotritia minima*, *Onychiurus armatus* and *Hoploclerema striculus*, which had a higher frequency and density in 1947.

Summarizing we may say that all species preferently inhabiting the F_x layer occur in all parts of the forest investigated microarthropods with a great population density in F_x (> 10 per 40 cm^3) are dispersed in this layer even in such a way that they occur in each or almost each sample of 40 cm^3 . For species, subferent in this layer (last ten species of table 14) this regular distribution is not proved. Experience, however, also points to a regular dispersal for these species within the forest.

From the fact of the regular dispersal of the species (high $F\%$) it may not be concluded that one sample would be sufficiently representative for the quantitative composition of the fauna of the forest soil. For this the densities of most species vary too much locally. For the investigation of the quantitative composition many sets of samples are required, all of them taken within the shortest time possible.

3. Seasonal Fluctuation

If we want to get to know the fluctuations of the microarthropod population in the layer of litter in the course of a year, it will have become clear from the preceding pages that we have to take into consideration the difference in composition of the fauna in the different layers of the forest soil, the downward migrations of the population during periods of drought and frost and the greatly varying local densities of most species. Examination of samples in which all layers are present would not yield an insight in these fluctuations, since the separate layers, as was already said in the description of the plot, often considerably differ in thickness over short distances. Moreover, samples in which all layers are represented would become too big for a minute analysis.

For this reason the investigation of the fluctuations was restricted to the F_x layer, in which microarthropods show their richest development both qualitatively and quantitatively.

In the middle of the forest, where the F_0 , F_1 and H layer were thin in comparison with the F_x layer, a surface of $1 \times 1\text{ m}$ was marked by means of four stakes. On this plot the thickness of the layers was rather constant over the whole surface. The F_0 , which was very loosely constructed was 2—3 cm high, the F_1 $1\frac{1}{2}$ cm, the F_x 4—6 cm and the H layer 2 cm. The latter still contained many litter particles.

From the F_x layer of this surface series of ten samples of 40 cm^3 were taken every two months, each series taking about 1% of the material originally present. It may be taken for granted that sampling to this degree did not disturb the composition of the microarthropod population. Influence of vertical migration on this composition may have been minimal in consequence of the comparatively thin layers of F_0 , F_1 and H. To maintain the circum-

stances as natural as possible no precautions were taken to prevent horizontal migration. However, it is not probable that this migration takes place to a great extent, most species inhabiting the F_x layer moving slowly. Thus the fluctuations in population density are mainly caused by birth and death of the individuals.

In choosing the interval between the dates of sampling the rapidity of the development of the Oribatei, being the most important group of microarthropods, served as guidance.

Literature about the rapidity of the development of the Oribatei is scarce. MICHAEL (1884, 1888), who bred numerous species, gives no detailed facts about this. HAARLØV (1942), investigating Oribatei in N.E.-Greenland where the vegetation period lasted from the end of May till the beginning of September, thinks he is justified to conclude to a course of development of one year for Oribatei, though his material did not exclude a period of development of two years. The fine observations of GRANDJEAN (1950) at *Camisia segnis* and *Platynothrus peltifer* proved development to take 150 or more days in these species in culture circumstances.

This slow development was also stated in experiments performed by Dr M. ROOSEBOOM in 1943 and 1944. The ecdyses of the larvae and nymphae took place with intervals of several weeks to some months even. Though attempts were made to keep the circumstances as natural as possible it is very likely that the development in nature is quicker. But it may be considered excluded that the development is so quick that the progress of the population density would not be expressed in bi-monthly samples.

Little is known too of the rapidity of development of the other groups of mites: Acaridiae, Parasitiformes, and Trombidiformes. In the first two groups phoresy occurs i.e. the nympha clings to other animals, which enables it to reach other places. It is clear that in this way no insight is gained in the development of the population, even if the intervals between the sampling tally with the rapidity of development. The time of development of many Trombidiformes is considerably shorter than that of the Oribatei.

In Collembola the rapidity of development seems to be greatly dependent on food and temperature. RIPPER (1930) and STREBEL (1932) give a time of development of 5—7 weeks for two species of *Hypogastrura* before the animals are mature. The total age can be 5—10 months. Though these data of course do not apply to all Poduromorpha they give an impression of the time of development that we may expect in edaphic collemboloes.

So the time of development of both Trombidiformes and Collembola may be considerably shorter than that of Oribatei. If this time of development is greatly influenced by environmental factors (feeding, humidity, temperature), as was proved for collemboloes, aggregations may arise under locally favourable conditions. Consequently, the density becomes very heterogeneous, and regular sampling gives no insight into the development of the population. This was the case with *Hypogastrura armata* e.g.

In order to get comparable values of the population densities on different times it was necessary to analyse the largest possible number of samples on each date of sampling. This number was fixed to 10. That this number is the minimum appears from comparison of the average densities with their standard-error respectively in 5 and 10 samples for *Nothrus silvestris* adult. In the first case this amounted to 13.4 ± 4.3 (coefficient of variation 0.71), in the second case 13.0 ± 2.6 (coeff. of var. 0.64). These values refer to the samples of the 31st January 1947. If we take this sample series together with that of the 7th February 1947, a series that does not yield a significant difference with the former because of the cessation in the development during this time, when the forest soil was frozen, we find as average density of the same species in these 20 samples 13.2 ± 1.5 (coeff. of var. 0.32). From this high coefficient of variation, even with a series of 20 samples, the rather heterogeneous density of the species concerned is clear. It is certainly not less heterogeneous in other species. Though a sample series of 20 would certainly have given more reliable values, for practical reasons the number had to be restricted to 10.

The series of samples were taken on March 19th, May 13th, July 30th, September 30th, November 30th 1946, January 31st and March 31st 1947. On 7th February 1947 a control series was taken during a frost period. These samples were just like those of the 31st January taken from material that was first defrosted. It appears that, in general, the results of the two series tally.

The general data on the climate (max. and min. temperature of the air, total precipitation per ten days), the average weights and water contents of the samples and the average densities in numbers per 40 cm^3 of the species are presented in fig. 10.

The average values of weights, water contents and densities are given as black columns. In all cases where there was sense in giving the range plus and minus $2 \times$ the standard-error, this was done. At the foot of the column the highest and the lowest value of the series of 10 observations are mentioned. In this way it is possible to get to some degree an impression of the variation of the separate values. The calculation of the standard-error is omitted in those cases in which the desiccation technique did not yield reliable values (weakly chitinized forms) and in the series in which o-values occurred more than twice. The widely divergent densities of the different species compelled us to use three different scales in vertical direction. The species follow each other from those with the greatest density to those with the smallest density. Species with a very heterogeneous density are shaded.

As far as possible juvenile and adult stages of the Oribatei were counted separately. Even all stages of *Nothrus silvestris* could be counted separately. It is remarkable that in all these species the juvenile animals fluctuate much more than the adults: *Nothrus silvestris*, *Hypochthonius rufulus*, *Tectocephus velatus*. Of some species none or only a very few juvenile animals were caught: *Oppia neerlandica*, *Belba minutissima*, *Oribatula tibialis*, *Chamobates schützi*, *Galumna* sp., *Phthiracarus borealis*, *Oribotritia loricata*. This phenomenon, which is also striking in the tables of FORSSLUND (1943) can, in my opinion, only be explained by the

incapability of the desiccation technique to drive out larvae and nymphae of many Oribatei, even when it is applied at the temperature of the room, and especially if the animals feed endophagously in litter.

Analysis of variance was applied to some objects viz. the air-dry weights and the numbers of *Oppia neerlandica*, Eremaeidae and the different stages of *Nothrus silvestris*. We found the following values for the variance ratio F:

Air-dry weights	11.9	<i>Nothrus silvestris</i> larva	8.08
<i>Oppia neerlandica</i>	0.68	— — nymph 1	12.61
		— — — 2	3.64
Eremaeidae	1.96	— — — 3	7.40
		— — adult	1.57 (2.60)

At the 5%, 1% and 0.1% point a value of F of 2.2 resp. 3.1 resp. 4.3 is significant. It appears that the variation of the averages of *Oppia neerlandica* and the other Eremaeidae (*Oppia* also belongs to this family) may be attributed to chance. In *Nothrus silvestris* this is only the case with the averages of the adults. This is caused by a very high number of specimens (68) in one of the samples of the July series, which has risen the error variance to an abnormal high value. If for this figure is substituted the average of the other nine samples of the series (14), F becomes 2.60 and then the variation is also significant on the 5% point. However the differences between the averages of the immature stages are much more significant. The significant differences of two succeeding averages are indicated in the diagrams by + at the foot of the columns.

The significant variation of the average air-dry weights, an object of which we might expect with certainty that it was to be attributed to chance only, requires further explanation. It appears that the averages of July and September 1946, and February and March 1947 are significantly higher than those of the other months. This difference might have been caused by taking the samples in these months deeper from the F_x layer, in consequence of which they might contain more humus and so have a higher weight with the same volume. However, the mutual comparison of all dry samples did not show any difference in the composition of the material. For the samples of July and September the cause of the difference may partly be found in the higher humidity of the air indoors in summer. With an air humidity of 70% the air-dry weight of litter of beech is about 5% higher than with a humidity of 50%. The averages of July and September lay, however, resp. 11% and 16% higher than the total average of March, May, November and January. Hence it seems probable that the samples of July and September are too much pressed together in the sampling box, so that their weights lie significantly higher than those of the other dates. As to the samples of February and March 1947 the difference in weight compared with the average weight of the samples of March, May, November, and January (resp. 9 and

SEASONAL FLUCTUATION OF MICROARTHROPODS



Fig. 10. Fluctuation in the density of microarthropods in the F_x layer of the beech forest 8 G.

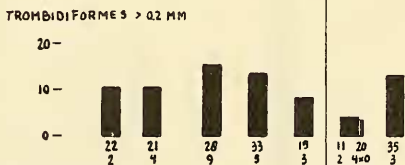
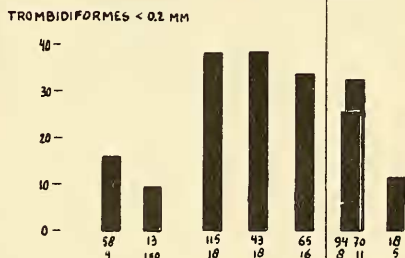
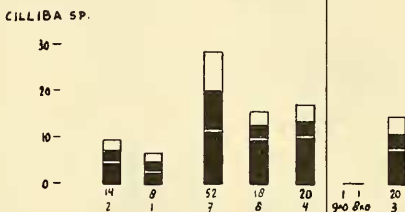
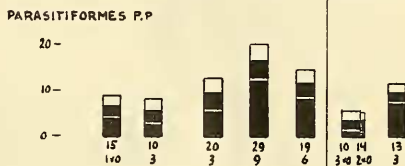
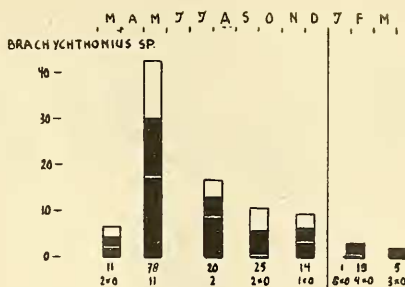
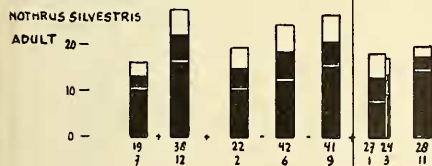
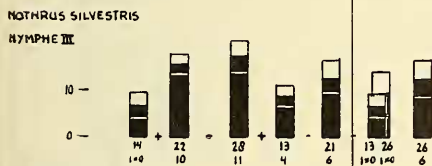
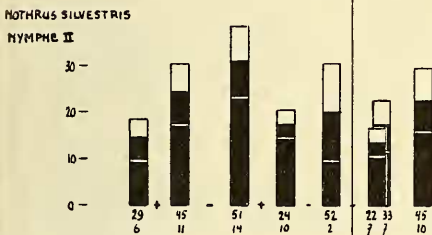
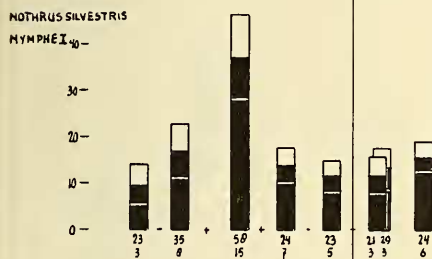
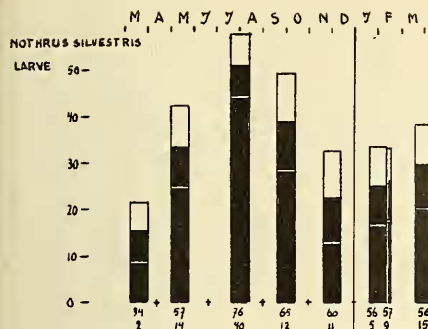


Fig. 10 (continued).

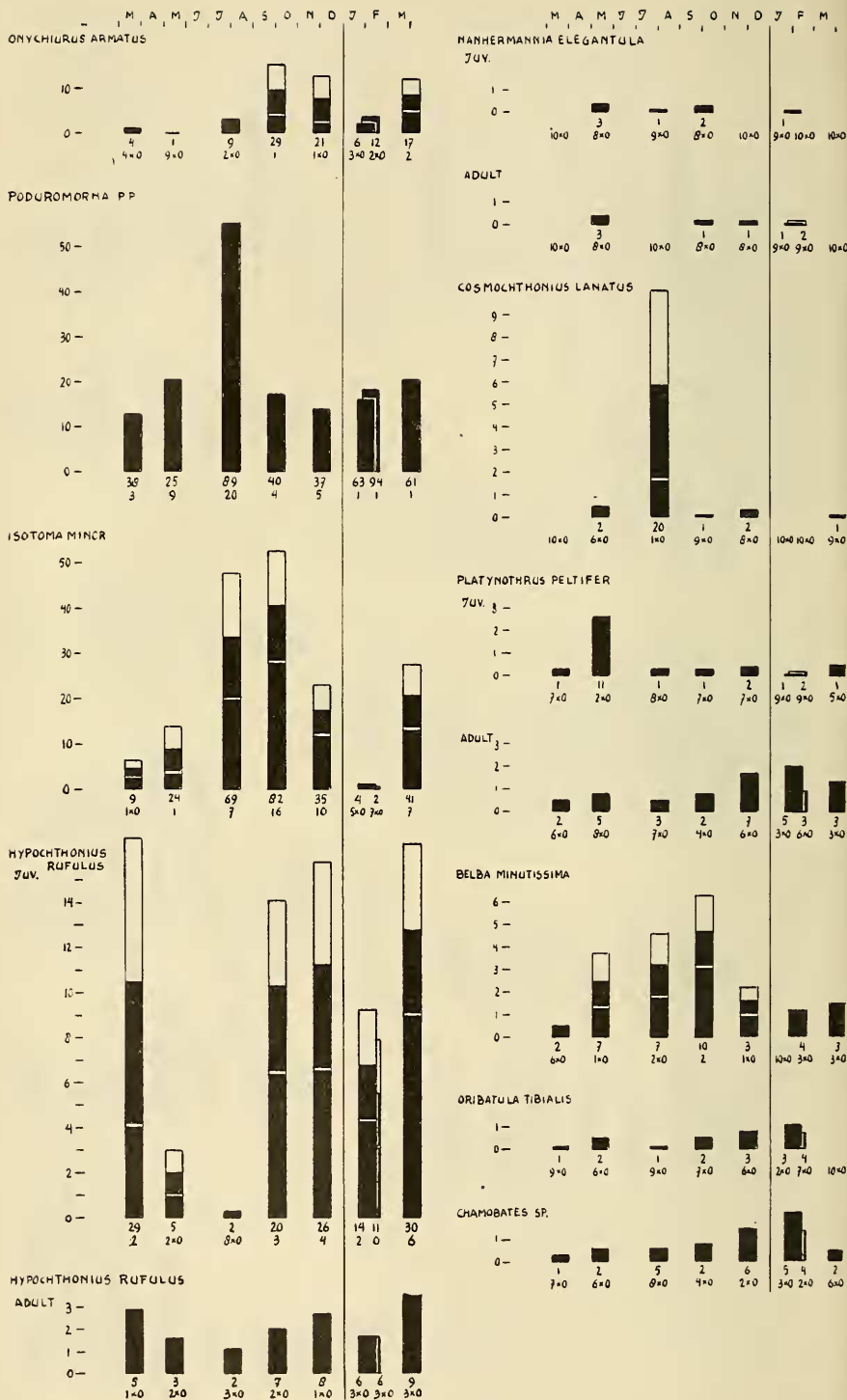


Fig. 10 (continued).

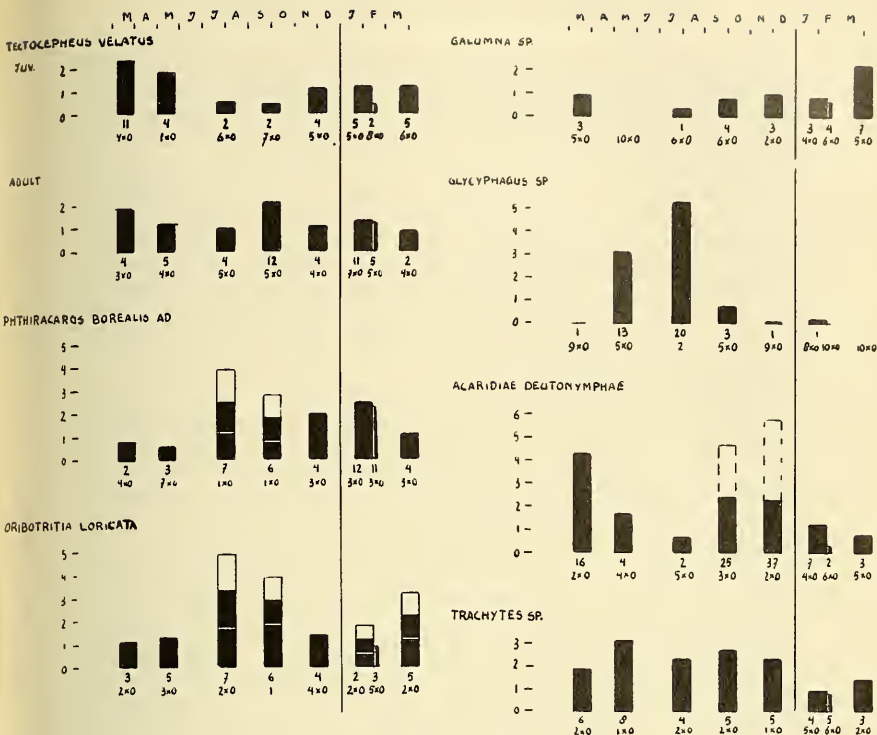


Fig. 10 (continued).

10%) should wholly be attributed to stronger pressing of the litter. Because of this mistake in the technique of sampling the average densities of the months of July and September 1946 and February and March 1947 should be diminished with 6, 11, 9 and 10%. In the diagrams this correction is not made. The general course of the population density of the species would hardly be influenced by this correction.

For a causal explanation of these fluctuations it is necessary to have knowledge in reproduction, time of development, life-time, influence of biotic and abiotic environmental factors etc. However, little is known about these things in the different species. So it is only possible to trace some correlation of the fluctuations with temperature and humidity (water contents).

An exact comparison of the course of the population with the temperature is not possible, since during the period of investigation only from the end of April to the middle of July 1946 the temperature of the layer of litter was recorded (see fig. 7). The data of fig. 7 and the temperature extremes given in the first diagram of fig. 10 enable us to form an idea of the course of the temperature

in the F_x layer investigated. The approximate course of the mean temperature in F_x is roughly given by the smooth curve in this diagram. The extremes between which the temperature varies daily differ mutually 2—4° C. In winter this temperature range may be still narrower.

The course of the population density of several species correlates in some degree with the course of the temperature: *Nothrus silvestris* juvenile stages, *Cilliba* sp., *Isotoma minor*, *Belba minutissima* and *Oribotritia loricata*. In the more detailed discussion of the development of the population of *Nothrus silvestris*, we shall see that in this case the reproduction is probably highest during the summer months. Experiments are needed to prove that this correlation is a causal one.

It must be emphasized that the long and severe frost period in general did not affect the population density of the species as appears from comparison of the densities in March 1947 (immediately after frost) with those in November 1946. Only some species decreased (*Oribatula tibialis*, *Chamobates schützi*), most species, however, maintained their density.

The humidity was rather equable during the whole year of investigation, as is shown by the diagrams of the precipitation and the water contents of the samples. Only the sampling date in May was preceded by a long dry period of 7 weeks, which clearly influenced the water contents of the samples. From the development of the population it does not appear that any species is influenced by these low water contents. The small numbers of juvenile *Hypochthonius rufulus* are very probably not a consequence of drought, since in May 1945 after a still longer period of drought and consequently with still smaller water content these animals occurred in specially great numbers.

In general the fluctuations have not resulted in a highly diverging density in March 1947 compared with that in March 1946. Most species have slightly increased in this period. Only in the cases of *Onychiurus armatus* and *Isotoma minor* an important increase is got. Wholesale development was not observed in any species. The small reproduction capacity, slow development and the varied composition of the community of the litter will prevent this in spite of the rich store of food.

b. Special Part

In the discussion of the most important species of the microarthropods following now, the Oribatei, being the most predominating group of inhabitants of the litter will be treated first. This will be done in the systematic order that WILLMANN (1931) gives in the 22nd part of "Die Tierwelt Deutschlands". Then the other groups of mites will be discussed and finally the collembolus as far as they are considered to belong to the microarthropods. As to nomenclature WILLMANN (1931) is followed for Oribatei, VITZTHUM (1929) for Acari non Oribatei and HANDSCHIN (1929)

for Collembola. In all species reference must be made to fig. 8 for normal vertical dispersal, to table 14 for horizontal dispersal (frequency), to fig. 10 for seasonal fluctuation and to table 13 for influence of drought and frost on vertical dispersal and mortality.

ORIBATEI

Nanhermannia elegantula Berl.

This species chiefly occurred in the F_x layer in an average density of 3 per 40 cm^3 . Larva, nympha and imago instars occur during the whole year. It has a rather high frequency ($F\%$): it occurs in about 60% of the F_x samples taken throughout the whole forest.

In the 80 F_x samples of the experimental surface of 1 m^2 it occurs only in 14% of the samples, moreover, in a small density, so that the course of the population is not very clear.

The species has a strongly marked preference for litter rather far decomposed, in which it probably feeds on this litter and on the moulds in it. In consequence of the small density in the forest examined, it is only of little importance there. It seems to be susceptible to drought: the density decreased strongly after a period of drought in August 1944 (see p. 68).

Hypochthonius rufulus Koch

A preference for the lower litter layers (both F_1 and F_x) is clear for the adults and juveniles. The average densities amount to 3 per 40 cm^3 for adults and 10—11 for juveniles. The species occurs in a very high frequency both in the whole forest (95%) and in the experimental surface of 1 m^2 (98%).

The fluctuations in the density of the adults are probably to be attributed to accident. The juveniles showed a low minimum in the early summer of 1946 in contrast to the early summer of 1944 when they showed a distinct maximum (table 13). This points to a different course of the fluctuation in density in the two years.

With extreme drought or frost the species is almost wanting in F_0 and F_1 , like all Oribatei that have their optimum in the lower litter layers.

What *Hypochthonius* feeds on is unknown. NOORDAM et al. (1943) managed to keep this species alive for 54 days without observing any feeding or deposition of excrements.

Brachychthonius Berl. sp.

These very small mites (length about 0.17 mm) have their greatest density in the F_x layer (an average of 12 per 40 cm^3) and occur here with a high frequency: they are found in 95% of the samples examined. In 1946 they had a distinct maximum in the early summer. The adults and the juveniles are counted together. On the analogy of *Nothrus* and *Hypochthonius* the young animals are probably the cause of the high top in spring. Of food nothing is known. In consequence of the very small size and the rather low numbers it is presumed to be of little importance. From the data of table 13 mortality in consequence of drought is thought probable.

Cosmochthonius lanatus (Mich.)

In general this species was only seldom met with ; in consequence there is little to say about the vertical and horizontal dispersal.

On the 1×1 m plot it developed in July 1946 a top amounting to about $12 \times$ the average density on the preceding sampling date on this plot. This top was followed again by a very low density on the next date of sampling. If this sudden increase is not caused by migration (in general improbable) or by a temporarily changed response of the species to the desiccation technique (in consequence of its life habits e.g.) it must be assumed that *Cosmochthonius lanatus* has largest short term fluctuations of all Oribatei, discussed in this paper.

Nothrus silvestris Nic.

Next to *Oppia neerlandica* this is the most abundant species of mites in the litter of the beech forest examined. Also in other deciduous woods this species was very numerous.

Both juvenile and adult animals have their greatest density in the F_x layer (annual average resp. 84 and 24 per 40 cm^3). Also in the H layer the animals may reach a rather high density, however. In all samples of every layer individuals of this species occurred, so that the frequency amounts to 100% for all layers. As it was possible for this species to count the larvae, the three nymphal instars and the adults separately, the course of the density of this species could be analysed approximately.

The larva was to be distinguished from the first nymphal instar by its three pairs of legs and its small size. On account of the size the different nymphal instars were identified, while the adults were recognizable by their size and their pigmentation. The average lengths of the different instars were: larva 0.32 mm, nymphal I 0.39 mm, II 0.48 mm, III 0.61 mm and adult 0.75 mm. With a magnifying power of $22 \times$ these instars could easily be distinguished. If there was some doubt between two instars the specimen was considered to belong to the group from the average of which it deviated least. But such dubious cases did not occur so often that they considerably reduced the reliability of the results.

By collecting the densities of the different instars in a graph we can visualize the development of the population and the way it was probably intermitted by a factor causing high mortality.

The observations and breeding experiments of Dr ROOSEBOOM made in our institute give us indications about the duration of the development of *Nothrus silvestris*. In an experimental series in which nymphae of the third instar were bred on F_x and H litter in circumstances that, in respect of temperature and humidity resembled the natural circumstances, 13 animals were bred. Of these 13 nymphae after one month none, after two months 5, after three months 9 and after four months 10 had moulted. Two animals had not yet shed their skins and one had died. So the greater number had moulted after 2 to 3 months.

In a second experimental series 20 animals of each instar were reared in favourable conditions. By using a great amount of litter in which the animals were reared it was only possible to detect part of the animals in the controls.

At a control after one month only some animals had moulted. After two months none of the 20 larvae were found; probably they died in the culture. Of the 20 nymphae I three were found, all passed into the second instar; of the 20 nymphae II 14 were found, 12 of them as nymphae III, the other two not yet moulted; of the 20 nymphae III three were found, all as adult animals; finally of the 20 adults 2 were found and also two larvae. At the following control only some ecdyses were observed, but none of the animals moulted for the second time. Mortality was very great now, so that we may assume that the circumstances were after all anything but natural, a reason why the development during the first months will have been slower than in natural circumstances. Though consequently no definite conclusions can be drawn from these breeding experiments as to the duration of the development of the different stages in nature, it is certain that this development is slow.

GRANDJEAN (1950) made detailed observations with regard to the duration of development in *Camisia segnis* and *Platynothrus peltifer*. He also stated a slow development in these species. From his results it is evident that the development in the successive stages requires increasing periods of time and that before moulting in each stage a period of immobility (periode pupale) occurs. Only with an exact knowledge of the duration of the developmental stages and the periods of immobility it is possible to follow the course of the population in detail: sampling intervals have to be in accordance with the development duration of the shortest stage (egg or larva stage), the length of the period of immobility influences the catching results.

The available data from bi-monthly sampling allow some insight in the course of the population from March to November (excluding winter samples for the extreme circumstances in which they were taken). The results of GRANDJEAN with the two related species mentioned above and those of Dr ROOSEBOOM with *Nothrus silvestris* suggest that the duration of the development in the earlier stages (larva and nymph I) takes a shorter time than the interval between two sampling dates and that the development of nymph II and nymph III requires periods which roughly correspond with this interval. If this is true the figures of nymphae II on each date and those of nymphae III on the next sampling dates refer to the same parts of the population and may be connected with each other in a graph. Figure 11 presents the corrected averages of the different stages (concerning the correction see p. 75). The figures of nymphae III and those of adults on the next date may not be connected as in the case of nymphae II and III. Next to nymphae III also the adults present on the same date lead to the numbers of the adults on the following date. (The adults can get more than one year old according to culture experiments.) So the added numbers of nymphae III and adults (dotted line) is to be connected with the adults on the next date.

The slight incline of the two lines from March to May has no real significance. Apparently no important mortality occurs in the stages concerned during this period. It does, however, from May to July and from July to September and to a less degree from September to November. Though comparable data on other stages fail, it is evident that at least from July to September also the other

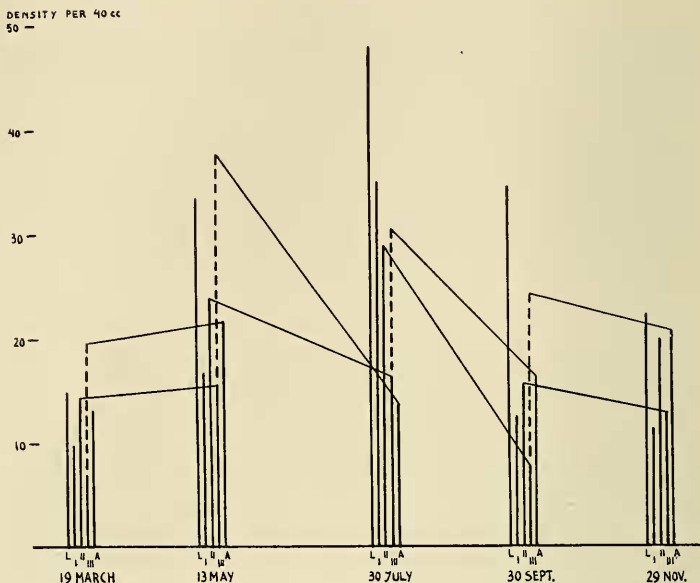


Fig. 11. The course of the population of *Nothrus silvestris* in the summer of 1946.

stages are liable to a heavy mortality. This mortality, active in all instars, makes it improbable that a predator is the cause of it. Besides, in breeding experiments, attacks of predators on Oribatei were never observed. Neither are climatic factors to be considered as cause. From the precipitation graph it appears that the whole summer was rather wet, so the litter was never strongly desiccated. This was only the case in the early summer when the average humidity of the May series amounted to 13.4 vol % against 30–35% on the other sampling dates. This drought, however, obviously did not check the development. This agrees with our experience in the very dry August of 1944. Then, in spite of still smaller humidity, no mortality of the adults and a great increase of young animals was observed. A parasitic attack must be considered the most probable cause of the mortality. VITZTHUM (1941) mentions as parasites: sporozoa (Haplosporidiae), gregarines and nematodes. Which of these parasites was the cause here is not known.

From fig. 11 it is evident that the larvae, notwithstanding their shortest duration of development, have the highest averages of all stages on all sampling dates. As the adults only fluctuate comparatively slightly it seems probable that reproduction is highest in July and is very low in November and March.

Like most Oribatei *Nothrus silvestris* responds to drought and frost by migrating from the F_0 and F_1 layer into lower layers.

In breeding experiments it feeds on litter, of which rather great quantities are eaten. On account of this feeding habit and the high

density this species is no doubt the most important mite for the decomposition of the litter in the beech forest investigated.

Platynothrus peltifer (Koch)

In consequence of the pronounced preference of this species for the upper litter layers frequency and seasonal fluctuation, both referring to the F_x layer, give an incorrect idea of the total population. In this layer the frequency is 30—40%. In the upper layers the frequency is no doubt higher. This appears from the data of table A (appendix), in which this species occurs in 14 out of the 15 samples of the F_0 layer ($F\%$ 93) and in 22 out of the 29 samples ($F\%$ 76) in the F_1 . The average density in F_0 amounts to about 8 per 40 cm³. The rather small number of young animals in proportion to the adults in the F_x layer is to be explained by the still greater preference of the young animals for the top layers.

This species, adapted to the climatic most extreme litter layer is less sensible to desiccation and frost and in contrast to most Oribatei it is still present in F_0 and F_1 in great drought and frost.

Platynothrus peltifer feeds on litter and is very well kept alive on it in experiments (NOORDAM et al. 1943). It was also observed by them to eat moulds. The density even in the upper litter layers is not yet great enough to expect a great influence on the decomposition of the litter.

Deposition of eggs, time of development and longevity in this species were studied by GRANDJEAN (1950). He estimates the total number of eggs deposited by one female to be more than 250. Development from larva to adult takes more than 150 days. Longevity of the adults exceeds 212 days.

Belba minutissima Sell.

This species has a distinct preference for F_x in which it occurred with a frequency of 30%. Considering the small density this dispersal is fairly regular. In the year 1946 the density appeared to increase from March to July and then to decrease quickly. In spite of the low average densities single observations in a series show such a great conformity that the averages are, no doubt, rather reliable and the fluctuations significant.

This species is supposed to be a mould eater like the larger species *Belba* cf. *verticillipes*, which occurs in the upper litter layers in a very small density. The latter species is closely related to *B. verticillipes* but it deviates by short spines on its back (identification of Drs L. VAN DER HAMMEN).

Oppia neerlandica (Oudms.)

This most abundant species occurred in all samples from all layers.

In the investigation into the vertical dispersal this species was taken together with the other Eremaeidae, which it greatly outnumbered. The maximal density for this species as for the whole family is in the F_x layer. Both in frost and drought the Eremaeidae

withdraw into the F_x and H layers, in which no significant mortality could be observed.

Especially for this very abundant species it is striking that only exceptionally juvenile animals were caught. FORSSLUND (1943) also mentions only adult animals in his tables. The absence of young animals is possibly to be attributed to a hidden or endophagous way of living.

In applying analysis of variance the fluctuations of the average numbers during the year 1946 appeared to yield no significant difference with the fluctuations of the single observations. So the fluctuations in the density may be attributed to accident.

Direct observations and investigation of stomach contents proved that *Oppia neerlandica* and several other Eremaeidae feed on moulds (ROOSEBOOM, not published). Because of their large density (about 160 per 40 cm³) it is very well possible that these species in decomposing mould hyphae, liberate important quantities of nitrogen, a function attributed to most animals of the soil by FORSSLUND (1943) and by him considered as their most important function.

Tectocephus velatus Mich.

Both juveniles and adults have their optimum in the F_1 and F_x layer. The species occurs in it with a frequency of about 70%. From the results of 1944—1945 (table A, appendix) it seems that this species should occur with greater density in the S. W. part of the forest (table A : A) than in the rest of it (table A : B, C, D and E). An investigation into the horizontal dispersal confirmed this (compare in table 14 I to II and III). However, from these densities and the frequency the difference between the parts appears to be less great than might be inferred from table A.

On the experimental surface of 1 m² the density of this species was only small. It is remarkable that in some samples the adults occur in a density 10 × larger than the average density in the remaining samples. This phenomenon also occurring in several samples from the series of 1944—1945 (e.g. 16 X 1945, 2) points to a local concentration, the cause of which is unknown. When we eliminate these high values the average density of the adults hardly appear to fluctuate. The juveniles had their largest density in spring.

Nothing is known to me about feeding habits.

Oribatula tibialis (Nic.)

This species has its largest density in the upper layers, reason why no clear idea is got of the horizontal dispersal and seasonal fluctuation.

The frequency in the F_x layer is only $\pm 10\%$; in the F_0 and F_1 layers the frequency is higher. Also in these top layers, however, the density is fairly small (1—2 per 40 cm³).

As with *Oppia neerlandica* very few juvenile animals were caught.

Even in great drought this species occurs in the upmost layers. With frost it does not withdraw either, as appears from its dispersal in the frozen layers of December 1945 and January 1946. That the species is almost wanting then in the F_0 layer possibly may be attributed to the fact that this newly fallen litter is not yet populated from the lower layers.

In connection with the above it seems improbable that the increase of the density in the F_x samples taken in the winter of 1947 is caused by immigration. This increase, which is small but still distinct, would then be attributable to an increase of the number of adult animals.

From the experiments of Dr ROOSEBOOM it is known that this species feeds on moulds.

Chamobates schützi (Oudms.)

As to the vertical dispersal and seasonal fluctuation the same can be said about this species as about the preceding. Of this species juveniles were not caught either.

Chamobates schützi has a distinct preference for the upper layers, which are not even left in drought and frost. The average density in this layer amounts to 4 per 40 cm³. Here too the fluctuation graph of the F_x layer shows a maximum in winter that must be a consequence of an increase of the adult animals.

According to the experiments of Dr ROOSEBOOM this species feeds on moulds.

Galumna cf dorsalis (Koch)

This form is related to *Galumna dorsalis* but is deviating by diverging interlamellar hairs (identification Drs L. VAN DER HAMMEN). The frequency in F_x is about 10%. In the experimental surface of 1 m² *Galumna* occurred more frequently viz. in 36 out of 80 samples (45%).

The high top of March 1947 in the fluctuation graph is caused by some samples with relatively high numbers for this species. Otherwise the graph does not show important differences in the densities.

In culture experiments of Dr ROOSEBOOM the species feed on moulds.

Phthiracarus borealis (Trägårdh)

This species has its optimum in the F_x layer and occurred in 45% of the F_x samples. The average density was considerably lower in the spring of 1946 than during the rest of the year. Then it remained at an equal height (about 2 per 40 cm³).

The small numbers in which this species is caught with drought and frost is probably due to a torpid state.

According to JACOT (1939) several young Phthiracaridae live in twigs, needles and under bark, which possibly would explain the scarce occurrence of young animals in the catches.

In breeding tests the adults decompose fairly large quantities of litter (NOORDAM et al. 1943).

Oribotritia loricata (Rathke)

This species prefers the lowest litter layer and the humus layer (4—6 per 40 cm³). The frequency is high (87%). In connection with their small density this points to a very regular horizontal dispersal.

The population has its highest density in summer. The young animals are caught in a much smaller number than the adults, this is probably to be attributed to their way of living.

Oribotritia was reared by Dr ROOSEBOOM on litter for several months.

Pseudotritia minima (Berl.)

This species has a pronounced preference for the humus layer. The average density here is about 27 per 40 cm³. For this reason it occurs little in the F_x layer: frequency 33%. In the autumn of 1947 the species occurred much more frequently here (93%) and sometimes in rather great densities too.

In the F_x samples of the experimental surface in 1946 it did not at all occur so that we have no data about the seasonal fluctuation.

On feeding habits nothing is known to me.

ACARIDIAE

Next to adults of the species *Glycyphagus domesticus* de Geer the heteromorphic deuto-nymphae of the Diacotricha are the most numerous representatives of Acaridiae in the litter layer of the forest investigated.

The second nymphal instar (deuto-nympha) in several families of the Acaridiae (Diacotricha) has a deviating form: mouth, intestinal canal, and anus are reduced or are absolutely wanting. This instar was not recognized by DUGES in 1834 as a deuto-nympha and was described by him as the genus *Hypopus*. Often these deuto-nymphae are still indicated by this name. These "Hypopods" (VITZTHUM 1941) can be developed as "Dauernymphe" or as "Wandernymphe". In the former case the animal is mostly surrounded by the skin of the proto-nympha, the suction pads — normally present on the body — are often wanting and the legs are badly developed. This "Dauernymphe" stage may last for a very long time and enables the individual to survive in unfavourable circumstances. It stands to reason that animals in such a state are not caught with a desiccation method. In the latter case ("Wandernymphe") the animal is suited for phoresy: by means of suction pads, claws and hairs it can attach itself to other animals and can so be moved to other places. Several arthropods and vertebrates can be used for this purpose.

The hypopod occurring most is the deuto-nympha of Anoitidae. It occurs in all litter layers but is very irregularly dispersed. Next

to samples in which hundreds of animals occur there are others in which they are absent. Hence little value can be attached to the averages calculated for the vertical dispersal and the course of the population.

The other hypopods occur in all layers but most in the lower litter layers. They occur less localized. In only two of the 80 samples of the 1 m² experimental plot aggregation was stated, resp. in September and November. In calculating the average densities for these months these samples were excluded. (The averages inclusive of these samples are dotted in the graph.) Whether the tops in this graph are real may be doubted. From observations of Dr ROOSEBOOM in breeding experiments it is known that free-living Thyroglyphidae can develop very quickly so that it is very well possible that there may be tops between the data of observation. Further it seems probable to me that for species appearing in aggregations small differences of the environment result in a varying time of development in these aggregations. For this reason countings in parallel samples have no sense for determining changes in the population.

Hypopods do not take any feed. FRANZ (1943) found that adults of *Rhizoglyphus echinopus* Fum. & Rob. feed on decomposed products of cellulose formed by bacteria.

Glycyphagus domesticus de Geer occurs in all layers usually in a very small density. In 1946 the population showed a maximum in July. It is, however, very well possible that this group develops more quickly than the Oribatei, so that some fluctuations remained unobserved because of bi-monthly sampling. The deuto-nymphae of this species were not caught: they belong to the so called "Dauernymphé", which are not caught with desiccation technique.

TROMBIDIFORMES

The often very small mites belonging to this group are not further distinguished. The desiccation technique is not effective for this group of small and delicate animals (see page 28). Consequently the real densities may lie considerably higher than the values found.

The group as a whole appears to be present in rather great numbers in all layers, the greatest density is found in the F_x layer (about 50 per 40 cm³), the frequency was 100% in all layers.

The fluctuations of the numbers in a year show a distinct minimum in spring for the small animals (up to 0.2 mm) while the larger animals fluctuate less. Here too tops in the population may not have appeared because of a quicker development of these species than that of the Oribatei. The greater part of the free-living Trombidiformes feed on prey: chiefly eggs, mites and collemboles. No doubt as predators they will greatly influence the community of the litter. The extent and the kind of the influence is, however, not yet stated.

PARASITIFORMES

Gamasides

Of this group the Parasitidae are the most important representatives in the litter layer. The species of the genera *Veigaia* and *Pergamasus* are most numerous.

This group also occurs in all litter layers, which agrees with its predatory way of living and its quick moving. Its density is about 8 per 40 cm³. Exclusive of the H it occurs in every sample of all layers. Only with drought and frost the animals retire from the upper litter layer.

Fairly distinct fluctuations in the density of the F_x layer could be stated in the year 1946. Since the juvenile instars of the Parasitiformes (larva, proto- and deuto-nympha) are well caught by the applied technique, this graph refers to the whole population with the exception of the deuto-nymphae of some species that attach themselves to other animals (chiefly arthropods) for dispersal purposes.

In the experiments of Dr ROOSEBOOM, thin-skinned mites, Dip-tera larvae and collembles were preyed on in great numbers by adults. Because of their large size and their enormous gluttony they are supposed to take an important place in the community in spite of their moderate density.

Uropodina

Cilliba v. Heyden sp.

This species occurs in all layers of the floor with a density of 6—12 per 40 cm³; only in the upper litter layer it has a smaller density. The frequency in the F_x layer is about 90%. The course of the population on the 1 × 1 m plot shows a density in summer 3—4 times higher than in spring; in winter the density decreases to 0 in the F_x layer, which may be explained by migration into the H layer. In the winter of 1945—1946 also an important movement from the F_x layer and the higher layers to the H layer was observed.

About food little is known with certainty. They are no predators nor saprophagous animals. Possibly they live on plant-saps, which is known of other Uropodina (FORSSLUND 1943).

Trachytes Mich. sp.

This species is only wanting in the H layer and has its optimum in the F₁ layer (6 per 40 cm³ on an average). With this density the frequency is about 90%. The seasonal fluctuations are of small extent, only in winter the population density is clearly smaller.

About food the same can be said as about the food of *Cilliba*.

COLLEMBOLA

Isotoma minor Schöff.

This is the only species of the Entomobryomorpha (as far as these belong to the microarthropods) which regularly occurs in

greater numbers in the forest floor examined. It has its optimum in the lowest litter layers in which it has an average density of 16 per 40 cm³. The frequency was about 90%. The graph of the density fluctuations shows a distinct top in summer. Nothing is known about the time of development. From what is known about the other species it seems, however, very improbable that the cycle takes a whole year. Because of the long intervals tops may have been cut out. It is, however, probable that the minimum in winter must be attributed to downward migration: just as for *Cilliba* we find a distinct withdrawal into the H layer in the winter of 1945—1946. With continuous drought the density of this species can decrease strongly, as was established in August 1944.

According to literature Collembola are little specific in their feeding habits. Both vegetable and animal substances, if soft, are eaten. Litter, moulds, algae, exuviae, dead animals are sources of food for most collembolids. Detailed observations on separate species are scarce (HANDSCHIN 1926, STREBEL 1932).

Poduromorpha p. p.

Into this group were taken all small Hypogastruridae, Achorutidae and Onychiuridae with the exception of the species *Hypogastrura armata* and *Onychiurus armatus*.

For the greater part the species present in the floor investigated are morphologically well fitted to subterranean life: pigment, eyes and furca are absent or reduced. The antennae are short, the covering with hairs is mostly scanty. VOLZ (1934) and GISIN (1943) consider species with these characteristics to represent a distinct "ecological type", the euedaphon, a term already introduced by KRAUSSE (1928).

The Poduromorpha concerned have their optimum very clearly in the lower layer of the floor. Here their frequency is 100%. The fluctuation graph shows a distinct maximum in the summer months possibly influenced by the damp months of May and June. In the severe winter of 1946—1947 their numbers did not decrease, as little as those of the other species. GLASGOW (1939), however, found that the severe winter of 1935—1936 had probably decimated the population of collembolids in the soil of a meadow.

In this group mortality is probable in consequence of drought (see p. 68).

According to literature the Poduromorpha feed themselves for the greater part on detritus and moulds.

With the other little collembolids they are supposed to form an important part of the staple-food in the litter layer.

Hypogastrura armata Nic.

The dispersal of this species is complementary to that of the other Poduromorpha: it has its optimum in the upper litter layers.

In contrast with the others pigmentation, furca and eyes are well developed and the body is densely haired. GISIN counts it among his "hemiedaphon". Because of its small density in the F

layers an incomplete idea of the horizontal dispersal and the seasonal fluctuation is given.

From the data of table A (appendix) it appears that the horizontal dispersal is an irregular one: individuals often occur in local aggregations. As with the Anoeidae for this reason the reliability of the averages is small and the fluctuation graph is greatly influenced by accident. (The diagram of this species in fig. 10 had to be shaded.)

STREBEL (1932) found in *Hypogastrura purpurascens* Lubb. "feeding and moulting communities" brought about by attraction by specific body scent. This may also be the cause of the aggregations in this species.

RIPPER (1930) established a time of development of 8—12 weeks (egg stage included) for *Hypogastrura manubrialis* Tullbg., a species very closely related to *Hypogastrura armata*. The term of life is 5—10 months. With intervals of 12—14 days eggs are produced in groups of about 30. Though these data may of course not be applied to *Hypogastrura armata* without further proof, it gives an idea of the possible order of the time of development etc. So it is very likely that this species produces some generations a year, which might explain the large local concentrations with animals of all sizes.

In contrast to other species of the collembolus *Hypogastrura armata* is little sensible to drought and frost. Even in extreme circumstances it maintains its optimum in the upper litter layers.

Onychiurus armatus Tullb.

This species, easily to be distinguished from the other Poduromorpha, also distinctly belongs to the type of the euedaphon. It is absent in the upper litter layer and occurs in the F_x layer in the greatest density (7 per 40 cm³). The frequency is about 70%.

Just as for the little Poduromorpha and *Isotoma minor* for this species mortality in consequence of great drought and a migration to the lowest layer with frost was established.

About the graph for the seasonal fluctuation the same may be said as about that of the other collembolus: it is very well possible that there are tops between the observations not occurring in the graphs.

GLASGOW (1939) actually found a number of tops in an investigation into the fluctuations of the density of this species in a meadow soil. However, it was not possible to state the numbers of generations from it.

Onychiurus armatus was bred by NOORDAM et al. (1943): the animals appeared feeding to fair extent on litter.

B. MESOFAUNA EXCLUSIVE OF MICROARTHROPODS

This group of the fauna, to which belong the nematodes, tardigrads and rotifers was only examined quantitatively on two dates. The species were not identified. The results of the countings are only presented to give an idea of the numbers in which these

animals may occur and the degree in which these numbers may vary from place to place.

Next to the groups just mentioned enchytraeids were also caught. Though belonging to the macrofauna they were still included because of their regular occurrence in fairly large numbers. Possibly because of the method applied these numbers are much greater than those from the desiccated samples of 4 dm³ (see following section).

In January 1947 in a short period of thaw ten samples of 40 cm³ from the humus layer of the beech forest 8 G were examined by plunging them into a funnel filled with water. Three of the samples failed, the results of the others are presented in table 15. The numbers found do not claim exactness, the effectiveness of the method was not checked.

Table 15. Enchytraeidae and mesofauna in samples of 40 cm³ from different layers of the floor of the beech forest 8 G.

Date	Layer	Enchytraeidae	Nematoda < 0.8 mm	Nematoda > 0.8 mm	Tardigrada	Rotatoria
20 I 1947	H	18	1200	46	8	1
	H	24	2550	160	100	27
	H	32	1900	65	12	2
	H	42	1200	68	—	7
	H	20	1800	95	13	2
	H	35	1230	280	81	40
	H	34	1050	185	65	18
21 II 1947	F ₀	—	342	21	81	87
	F ₁	1	1160	53	17	23
	F ₁	—	785	50	17	26
	F _x	1	1022	8	4	2
	F _x -H	5	2655	61	2	26

From the table it appears, however, that the density of the nematodes may outnumber that of the mites and collembolus by far. Especially the nematodes smaller than 0.8 mm are very numerous. Tardigrads and rotifers occur less numerous. It may be, however, that the method is less effective for these species.

In February 1947 one sample of the F₀, two of the F₁ and two of the F_x-H layer were defrosted and likewise examined: see table 15.

Though the numbers in the different samples of one layer strongly fluctuate it may be taken for granted that nematodes have a minimal density in the F₀ layer. The rotifers occurred in maximal numbers in this layer.

From the numbers in which the nematodes occurred may be supposed that they have an important place in the community of the litter. For a detailed investigation into this matter it is necessary to identify the species and, if possible, to breed them, for which there was no opportunity.

FRANZ (1942) made it plausible that several nematodes (species of *Diplogaster* and *Rhabditis*) play an active part in the aerobic decomposition process of cellulose¹).

According to the same author the tardigrad *Macrotrachela concinna* occurs in great numbers on filter paper laid on stable manure so that in this species also participation in the decomposition of cellulose is presumed.

According to literature rotifers feed on algae, diatoms, protozoans and detritus particles, which are carried into the mouth-opening by a water-current caused by cilia. In desiccation of the substrate the rotifers, like the groups mentioned above, change into an anabiotic condition, which enables them to survive extreme circumstances.

C. HEMIEDAPHIC MACROFAUNA

In this group of the soil fauna, caught by means of desiccating samples of 4 dm³, three phyla of the Animal Kingdom are represented in the forest floor investigated: the Annelida, the Mollusca, and the Arthropoda.

Of the Annelida only two families of the order Oligochaeta are represented viz. Enchytraeidae (potworms) and Lumbricidae (earthworms).

The Mollusca are represented by some families of the Pulmonata: slugs and snails.

The bulk of the macrofauna belongs to the phylum Arthropoda in the classes Crustacea, Arachnoidea, Progoneata, Chilopoda and Hexapoda.

The Crustacea are represented only by the order Isopoda (woodlice).

Of the Arachnoidea three orders are represented: Araneina (spiders), Chernetes (false scorpions) and Opiliones (harvesters), the first order by several families, the second by one family only, the Obisiidae, and the third by two families: Phalangidae and Nemastomatidae.

The classes Progoneata and Chilopoda can be taken together as Myriapoda. Of the first the Diplopoda (millipedes) and Symphyla, of the second (centipedes) the Geophilomorpha and the Lithobiomorpha are the only representatives.

At last the classis Hexapoda (Insecta) is represented by many orders: Diplura (bristle tails), Protura, Collembola (spring tails), Orthoptera (cockroaches, grasshoppers, crickets), Dermaptera (earwigs), Corrodentia (psocids), Rhynchota (bugs), Thysanop-

¹) In a recent paper (Veröffentlichungen der Bundesanstalt für Alpine Landwirtschaft in Admont H. 2, Wien, 1950) FRANZ abandons this view and thinks that these nematodes feed on bacteria.

tera (thrips), Coleoptera (beetles), Hymenoptera (ants, ichneumonflies), Diptera (midges and flies) and Lepidoptera (butterflies and moths). Of these orders several are represented by a very small number of individuals only: Orthoptera, Dermaptera Corrodentia and Thysanoptera. They are left out of account here.

That each of the groups was not collected with the same exactness was already stressed in discussing the technique (see p. 34). For several groups we shall return to this matter.

a. General Part

During the year 1946 and in the first three months of 1947 standing out by an extremely severe frost, in total 96 samples of 4 dm³ from different layers of the beech forest floor were examined quantitatively by the technique of desiccation. Not all layers were sampled to the same extent. Of the F₀ layer and the top layer of the mineral soil, containing a small population in general, a smaller number of samples was examined than of the other layers. Because of the relatively small number of samples too little data are available for reliable conclusions as to the horizontal dispersal and the fluctuation of the macroarthropods. So these sections are omitted here. Only some observations on local concentrations will be mentioned (p. 96). Phenological data and data concerning development are discussed in a separate section.

Owing to their greater size and mobility it is to be expected that the macroarthropods are less strictly bound to the thin, well defined litter layers than the microarthropods.

In contrast to the sets of 40 cm³ samples, the separate samples of which were taken from the different layers (F₀, F₁, F_x, H) as homogeneous as possible, the sets of 4 dm³ samples contained the whole organic layer and the top layer of the mineral substrate on the spot of sampling. So the transitional layers are included in the samples and the differences between the samples in a set are less marked. F₀ refers to the same layer as in the case of microarthropods: the loose layer of litter fallen during the last autumn. F is the litter layer below F₀ that is decomposing, but the elements of which have not yet fallen asunder into small particles. H is the layer in which this is the case and which consists of amorphous humus for the greater part. A₁ is the top layer of the mineral substrate.

Dependent on the thickness of the layers the samples of one set have a varying surface. In general the surface of the F₀ samples was largest (about 80 × 80 cm); the surfaces of the H and the A₁ samples, which were always taken the same were smallest (about 40 × 40 cm).

With the intention to gain some insight into the cycle of life of the species the animals were classified according to size. For limits of these classes the following logarithmic scale was used:

Classes of sizes:	0	I	II	III	IV	
Limits:		2	4	8	16	mm

Thus each class contains animals up to 4 times larger in length than the animals of the preceding class.

It is clear that this classification is a very rough one especially for those species, varying in size within two classes only. For each species the ideal classification would be the one where each class represents an instar. In this investigation we had to be content with the classification mentioned.

In table B (appendix) the data of January 1946—December 1946 are inserted. The results of the samples in the frost period of January-February 1947 are more or less deviating and are separately dealt with.

At the top of the table the air-dry weights and the water contents in percentages of the volumes have been given.

In each of the layers the air-dry weights of the samples appear to differ in a high degree. Because of the rather rough differentiation of the layers this is to be expected. Especially samples in the H and A₁ layer may show great differences in weight because of locally higher contents of sand, humus, and roots.

As a matter of fact the water contents depend on meteorological circumstances. The samples of May appear to have been the driest, taken after a period of drought of about 5 weeks, the wettest were the samples of November and December. The vertical dispersal of the species in the F, H and A₁ layers appears not distinctly to differ on the two dates. Still this difference might have appeared with a greater number of samples.

This table also shows the tendency of several species to form local concentrations often not restricted to one layer. This is clear e.g. with the Geophilidae in the second set of samples of May in which all classes of size of this group occur in rather large numbers, especially in the F and H layers. The enchytraeids (samples of November and December), the larvae of the Anthomyiidae (winter samples) and particularly the larvae of the Sciaridae (March, May, July) also show this phenomenon of local concentration.

In general the samples or sets of samples were taken at random throughout the forest. Only the six samples of August (both of the F and H layer) and the three sets of samples of October were taken immediately next to each other. A mutual comparison of the six resp. three samples shows the homogeneity of the dispersal on a small surface: the composition of the fauna in these parallel samples agrees highly.

1. Vertical Dispersal

From the data summarized in table B it is possible to get some information about the vertical dispersal of the species in the floor by calculating their average density per 4 dm³ for each layer. For species or stages of species only appearing during part of the year, the description of the vertical dispersal must be restricted to the period in which the individuals concerned occur. To avoid over-estimation of the series of August and October, the samples of each taken from the same spot, the data of these series were aver-

Table 16. Density per 4 dm³ and per m² of the different classes of size of the macrofauna species in the different layers of the floor. Except where Roman numerals at the top of a column indicate a restriction to a certain part of the year (e.g. XI—III: averages restricted to November to March inclusive) all averages are annual.

Classes of size limits in mm		Density per 4 dm ³						Density per m ²							
		O	I	II	III	IV	Total	O	I	II	III	IV	Total		
		2	4	8	16			2	4	8	16				
<i>Dendrobaena octaedra</i>	F ₀				XI-III	0.2	1.6	1.6				XI-III	0.3	2.6	2.6
	F					2.6	6.1	6.1					6.9	16.3	16.3
	H					0.3	1.9	1.9					1.4	10.5	10.5
	A ₁					0.3	0.2	0.2					1.8	0.9	0.9
													10	30	30 (+ 10)
<i>Arion subfuscus</i>	F ₀			0.4	1.1	1.1	2.6			0.6	1.7	1.7	4.0		
	F			0.7	0.9	—	1.6			1.9	2.5	—	4.4		
	H			0.2	0.2	0.1	0.5			1.0	1.0	0.7	2.7		
	A ₁			—	0.5	—	1.5			—	2.8	—	2.8		
										4	8	2	14		
<i>Lithobius calcaratus</i>	F ₀		VII	—	—	0.1	—	0.1		VII	—	—	0.2	—	0.2
	F		—	0.6	0.2	0.1	0.9			—	1.5	0.6	0.4	2.5	
	H		1.8	0.3	0.1	—	0.4			9.6	1.4	0.9	—	2.3	
	A ₁		—	0.3	—	—	0.3			—	1.8	—	—	1.8	
										10	5	2	—	7 (+ 10)	
Geophilidae	F ₀			—	—	—	—			—	—	—	—	—	
	F			0.3	0.9	0.6	1.8			0.8	2.3	1.7	4.8		
	H			3.1	7.9	2.1	13.1			17.2	43.7	11.3	72.2		
	A ₁			2.5	3.7	11.0	17.2			13.8	20.2	60.5	94.5		
										32	66	74	172		
<i>Cylindrojulus silvarum</i>	F ₀		—	0.7	—	0.2	0.9			—	1.1	—	0.3	1.4	
	F		1.1	2.1	1.1	0.9	5.2			3.0	5.7	3.0	2.5	14.2	
	H		2.2	3.5	2.2	1.6	9.5			12.0	19.3	12.0	8.9	52.2	
	A ₁		—	1.0	0.7	0.5	2.2			—	5.5	3.7	2.8	12.0	
										15	32	19	15	80	
<i>Campodea staphylinus</i>	F ₀		—				—			—				—	
	F		0.6				0.6			1.5				1.5	
	H		10.1				10.1			59.1				59.1	
	A ₁		23.0				23.0			126.5				126.5	
										187				187	
Entomobryomorpha	F ₀	11.2	2.6	0.4			14.2	17.9	4.2	0.7			22.8		
	F	17.6	5.9	1.0			24.5	47.0	15.8	2.7			65.5		
	H	1.2	1.2	0.1			2.5	6.5	6.5	—			13.3		
	A ₁	—	0.3	—			0.3	—	1.8	—			1.8		
								71	28	4			103		

Table 16 (continued).

Classes of size limits in mm		Density per 4 dm ³						Density per m ²						
		O	I	II	III	IV	Total	O	I	II	III	IV	Total	
		2	4	8	16			2	4	8	16			
Incurva- riidae	F ₀		VII (1.2)	0.3			0.3			0.5			0.5	
	F		(1.4)	4.6			4.6			12.2			12.2	
	H		(1.0)	0.7			0.7			3.8			3.8	
	A ₁			0.3			0.3			1.8			1.8	
										18			18	
Staphylini- dae l.	F ₀		4.4	2.4	0.2	—	7.0		7.1	3.9	0.3	—	11.3	
	F		4.9	3.9	0.5	—	9.3		13.0	10.5	1.3	—	24.8	
	H		5.2	3.6	0.9	0.2	9.7		28.5	19.6	4.8	1.0	53.9	
	A ₁		0.5	1.8	0.3	0.7	2.6		2.8	10.1	1.8	3.7	18.4	
								51	44	8	5		108	
Staphylini- dae im.	F ₀		2.1	1.1	—		3.2		3.4	1.8	—		5.2	
	F		15.5	4.1	0.6		20.2		41.3	11.5	1.7		54.5	
	H		3.3	3.6	1.1		8.0		18.2	19.9	5.8		43.9	
	A ₁		1.2	1.2	—		2.4		6.4	6.4	—		12.8	
								69	40	8			116	
Cantharidae l.	F ₀	VIII-X	—	0.4	0.2	—	0.6		0.6	0.3	—		0.9	
	F		(3)	9.2	2.9	3.4	12.1		24.5	7.8	9.1		32.3	
	H		(20)	6.4	1.9	1.0	8.3		35.1	10.7	5.5		45.8	
	A ₁		—	2.7	0.8	—	3.5		14.7	4.6	—		19.3	
								75	23	15			98 (+ 15)	
<i>Athous sub- fuscus</i> l.	F ₀	VIII	—	0.1	—	0.1	0.2		0.1	—	0.2	I-III	0.3	
	F		—	0.3	2.0	2.6	0.4	4.9	0.8	5.3	7.0	1.1	13.1	
	H		(4)	7.4	14.2	3.8	0.2	25.4	40.9	78.0	20.6	1.1	139.5	
	A ₁		—	5.3	6.2	0.6	0.5	12.1	27.7	33.9	3.7	2.8	65.3	
									70	117	32	5	218 (+ 5)	
Pentatomi- dae	F ₀			VIII-III	1.0					VIII-III				
	F				1.5					1.6				
	H				0.3					3.9				
	A ₁				0.3					1.8				
										1.8				
<i>Rhagio li- neola</i> l.	F ₀	VIII-XI	—	XI-VI	I-VIII	1.4	0.2		VIII-XI	XI-VI	I-VIII		0.3	
	F		—	0.6	3.2		2.6		—	1.7	8.6		6.9	
	H		1.0	1.5	4.9		5.3		5.5	8.5	27.1		28.9	
	A ₁		—	0.6	4.0		4.0		—	3.7	22.0		22.0	
									6	14	58		58	
<i>Phaenocla- dius</i> sp. l.	F ₀	XII V	16.7						XII-V					
	F		3.1						26.7					
	H		1.0						8.3					
	A ₁		1.6						6.2					
									8.8					
								50						

Table 16 (continued).

Classes of size limits in mm		Density per 4 dm ³						Density per m ²					
		O	I	II	III	IV	Total	O	I	II	III	IV	Total
		2	4	8	16			2	4	8	16		
Anthomyi- dae 1.	F ₀		XI	XII-III			XI-III			XII-III			XI-III
			56	34.1			37.8			54.6			60.4
	F		0.5	23.0			23.0			61.3			61.3
	H			1.8			1.8			9.6			9.6
	A ₁			—			—			—			—
										126			131
<i>Fannia</i> sp. 1.	F ₀			1.0			1.0			1.6			1.6
				1.4			1.4			3.6			3.6
	H			0.3			0.3			1.7			1.7
	A ₁			0.2			0.2			0.9			0.9
										8			8
<i>Obisium muscorum</i>	F ₀		2.2				2.2		3.5				3.5
			1.1				1.1		2.9				2.9
	F		0.3				0.3		1.4				1.4
	H						—		—				—
	A ₁						—		—				—
									8				8
Araneina	F ₀	2.3	5.2	0.8	0.3		8.6	3.7	8.3	1.3	0.5		13.8
		10.4	6.6	0.2	0.1		17.3	27.6	17.5	0.5	0.2		45.8
	H	12.2	7.3	0.9	—		20.4	58.8	40.2	4.8	—		103.8
	A ₁	6.3	5.8	0.2	—		12.3	34.8	32.1	0.9	—		67.8
							125	98	8	1			231

aged and the averages were considered to be simple data in calculating the total average.

In table C (appendix) the data of the most important species ranged according to their classes of size are presented. The average densities calculated from these data occur in table 16, left part. By adding together the values of all classes of size of a species occurring throughout the year a total idea of the vertical dispersal of that species was obtained.

These total values are represented graphically in fig. 12.

Of *Rhagio lineola*, having a development of one year and of the Anthomyiidae only occurring from November to March, the values of the vertical dispersal were calculated from the numbers of all larval instars in the samples during the period of occurrence.

If we compare the vertical dispersal of the different classes of size of a species (table 16) it appears that these are fairly well the same. Only in the Geophilidae there are differences: animals measuring 4—16 mm have their maximum in the H layer, the larger animals however in the A₁. This is probably caused by the presence of two species one measuring 16 mm at most (*Brachygeophilus truncorum*), the other measuring up to 22 mm (*Schendyla nemorenensis*).

Fig. 12 shows that most species have a specific dispersal in the

different layers of the floor. In this respect most pronounced are the Diptera larvae *Phaenocladus* sp. and Anthomyidae, *Arion subfuscus* and the Entomobryomorpha distinctly preferring the upper litter layers, *Dendrobaena octaedra* and the larvae of the Incurvariidae having their optimum in the F layer, *Campodea staphylinus* and the larvae of *Athous subfuscus* chiefly inhabiting the humus layer and the adjoining A_1 layer.

In order to make the values comparable with data from other sources it is desirable to express these densities also per unit of surface (e.g. 1 m^2) of average composition with regard to thickness

VERTICAL DISTRIBUTION OF MACROFAUNA IN BEECH FOREST FLOOR

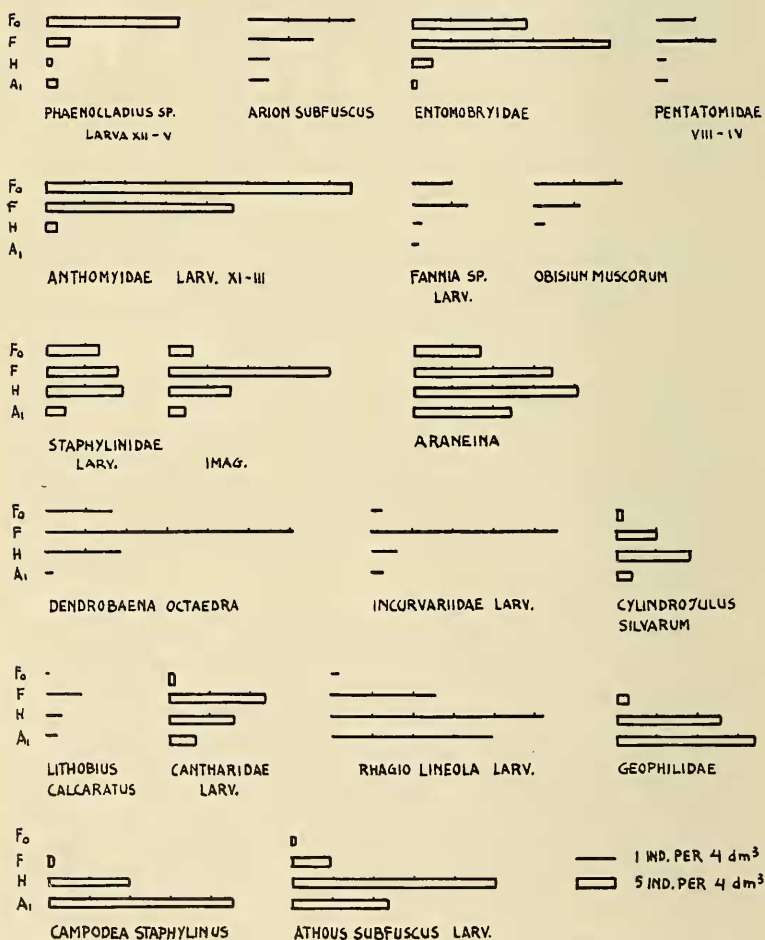


Fig. 12. Vertical dispersal of the macrofauna in the floor of the beech forest 8 G.

of the layers. To obtain this we have to multiply the numbers found per 4 dm³ with a certain coefficient which is different for each layer. These coefficients were deduced from the surface taken up by the material of a number of samples of 4 dm³, taken throughout the forest. Unfortunately, only a small number of sample surfaces were measured. So the averages have high standard deviations and give only rough approximations of the average composition of the floor. Table 17 gives these surfaces, their averages and the approxi-

Table 17. Surfaces of some 4 dm³ samples from the F₀, F, H and A₁ layer in m² and the coefficients for calculating the density per m² from the density per 4 dm³.

Date	F ₀	F	H and A ₁
9 VIII '46			$0.25 \times 0.5 = 0.13$
3 X '46		$0.5 \times 0.75 = 0.38$	
19 XI '46	$0.8 \times 0.6 = 0.48$	$0.8 \times 0.7 = 0.56$	$0.5 \times 0.4 = 0.20$
—	$0.8 \times 0.6 = 0.48$	$0.7 \times 0.4 = 0.28$	$0.6 \times 0.4 = 0.24$
5-13 XII '46	$0.8 \times 0.8 = 0.64$	$0.5 \times 0.5 = 0.25$	$0.4 \times 0.4 = 0.16$
—	$0.8 \times 0.8 = 0.64$	$0.6 \times 0.6 = 0.36$	
—	$1.0 \times 1.0 = 1.00$		
—	$0.7 \times 0.7 = 0.49$		
Average	0.62 ± 0.08	0.37 ± 0.05	0.18 ± 0.02
Approximate coefficients for calculating the density per m ²	8/5	8/3	11/2
Real values of these coefficients lying between	$0.8 \times$ and $1.35 \times$	$0.8 \times$ and $1.4 \times$	$0.8 \times$ and $1.3 \times$
			the approximate values

mate coefficients inferred from them for the different layers. They are the same for samples of the H and A₁ layer since the same surface was used for both. From the average surfaces plus and minus 2 × the standard deviation the limits of the real values were fixed with respect to those calculated with the approximate coefficient. The difference between the real value and the value calculated may amount to 20—40% of the latter. So the numbers calculated per m² only possess a small exactness.

In table 16 (right part) the numbers per m² are given for the different classes of size and the total numbers of each species or group in the different layers.

The added numbers for all layers (rounded off to whole numbers) give a rough idea of the density of the different classes of size and the total density of each species (group) on 1 m² forest floor of average composition.

To find out where the litter fauna stays in a frozen floor samples were cut out during the severe frost period of 1947 (see fig. 10, first graph) on 8th and 31st January, 20th February and 8th March. As it was impracticable to take samples of 4 dm³ from the frozen substrate the samples were taken amply, carried to the laboratory

in a bag, slowly thawed there, reduced to a volume of 4 dm³ and desiccated in the ordinary way. In a short period of thaw lasting from 9th to 23rd January four not-frozen H samples were taken (20th Jan.). The average numbers of animals caught in three sets of frozen samples, the averages established in three sets of samples in November and December 1946 and the averages of two sets of samples of 24th March, taken immediately after the frost had disappeared from the soil, are given in table 18. Moreover the values of the average density in the four samples from the H layer on 20th January, when the floor was thawed, are inserted. All averages have been calculated from values only slightly differing from each other. Only some averages of *Cylindrojulus* and *Cantharidae* refer to data mutually differing very much because of the occurrence of an abnormally high number of animals in one of the samples (local concentration). These values are italicized and are of little value for comparison. Geophilidae and some other groups with a very heterogeneous density were wholly left out of consideration for this reason.

Though the averages of November-December, the frost period and 24th March only refer to resp. 3, 3, and 2 data they still give a rather correct impression of the vertical dispersal. For the values of November-December and March this appears from the fact that the vertical dispersal satisfactorily agrees with the dispersal as this is represented for the different species in fig. 12. For the data of the winter this appears from the agreement of the values for H and A₁ with those inserted in parentheses behind them. These are the averages of 10 resp. 7 samples from the H and A₁ layers examined during this frost period.

In comparing the averages in autumn, winter and spring the catches of the upper layers in winter appear to be considerably lower than those of the same layers in autumn and spring. Exceptions are *Incurvariidae*, *Rhagio* and *Phaenocladus*. The catches in the lower layers of the floor generally differ less with those before and after the period of frost.

If the fauna had withdrawn into the lower layers of the floor because of the frost, we should have expected higher catches in these layers especially of those species that have their optimum in the upper layers: *Dendrobaena*, Staphylinidae, Araneina. That these animals did not flee from the frost by withdrawing into the non-frozen subsoil was shown by the examination of a number of these samples: hardly any of these animals were caught in it.

Other explanations of the small catches in the frozen samples may be great mortality because of the low temperature and diapause.

In the case of mortality the density of the population after the frost should be of the same order as during the frost and considerably lower than in autumn. This appears only to be true for some species: Staphylinidae imagines and *Acrotrichis* appeared after the frost in a much smaller density than in autumn. Besides the influence of the frost this may be very probably connected with

Table 18. Vertical dispersal of the macrofauna in the frozen floor in the winter of 1947 compared with that in November-December 1946, before frost and that in March 1947, immediately after frost. Densities in numbers per 4 dm³.

		Nov.-Dec 1946	Winter 1947	20th Jan. 1947	March 1947
<i>Dendrobaena octaedra</i>	F ₀	0.7	—		2.0
	F	11.0	—		6.5
	H	1.3	1.0 (1.2)	3.0	—
	A ₁	—	— (—)		—
<i>Cylindrojulus silvarum</i>	F ₀	—	—		2.0
	F	2.0	2.0		13.5
	H	9.7	1.3 (3.1)	23.8	27.5
	A ₁	3.0	1.0 (1.1)		7.5
Entomobryomorpha	F ₀	12.3	0.3		19.0
	F	45.0	6.7		22.5
	H	1.0	0.7 (0.9)	0.1	1.5
	A ₁	—	— (0.6)		0.5
Incurvariidae	F ₀	—	—		—
	F	5.3	6.7		6.0
	H	0.7	0.3 (0.1)	2.3	0.5
	A ₁	—	0.3 (0.3)		—
Staphylinidae l.	F ₀	3.0	—		2.0
	F	16.3	2.7		6.5
	H	9.7	5.7 (5.1)	17.8	8.0
	A ₁	1.0	1.5 (2.7)		6.5
Staphylinidae im.	F ₀	3.3	0.3		2.5
	F	50.7	7.7		28.5
	H	5.0	5.7 (3.8)	8.0	5.5
	A ₁	1.0	2.5 (1.9)		1.5
<i>Acrotrichis</i> sp.	F ₀	4.0	—		3.5
	F	39.0	0.7		8.5
	H	0.3	0.7 (0.6)	0.5	—
	A ₁	—	— (—)		0.5
Cantharidae l.	F ₀	0.3	0.3		2.0
	F	15.0	1.3		12.5
	H	9.3	28.3 (12.3)	27.0	3.0
	A ₁	5.0	4.7 (2.7)		1.0
<i>Athous subfuscus</i> l.	F ₀	—	—		2.5
	F	4.3	—		3.0
	H	15.7	12.0 (11.4)	12.8	16.5
	A ₁	13.0	1.0 (2.0)		10.5
<i>Rhagio lineola</i> l.	F ₀	—	—		—
	F	—	0.7		1.0
	H	1.0	5.7 (5.4)	2.5	4.0
	A ₁	—	13.0 (6.1)		6.0
<i>Phaenocladus</i> sp. l.	F ₀	3.0	0.7		1.5
	F	—	3.3		—
	H	—	— (—)	0.3	—
	A ₁	—	— (—)		—
Anthomyidae l.	F ₀	61.7	3.3		7.0
	F	20.3	10.0		11.5
	H	1.0	— (—)	1.5	—
	A ₁	—	— (0.3)		—
Araneina	F ₀	7.0	—		3.0
	F	25.0	1.3		16.5
	H	17.7	1.7 (5.1)	7.0	8.5
	A ₁	—	1.0 (0.7)		1.0

the cycle of life of certain species : mortality of the imagines before winter. Also the larvae of Anthomyidae have highly decreased in density. In this case the possibility is not excluded that part of the larvae already pupated before the frost.

Nor diapause is probable in the species concerned. If we compare the average numbers of animals caught in the H layer during frost with those caught on 20th January (period of thaw) it appears, in species that occur in smallest numbers in frozen samples, that the values at thaw lie considerably higher than those of the frozen samples. If diapause occurred the numbers at thaw had been small too.

The only explanation for the small catches in frost seems to be found in the sampling and desiccation technique applied to frozen samples. From the numbers caught in the H samples on 20th January it may be concluded that the density of the fauna in the H layer is relatively high. From this we must assume that samples taken in frozen condition, thawed artificially and then desiccated, only yield a small part of the animals present. The cause of it is unknown. If this is true, from the results of the frozen winter samples no reliable information can be got with regard to the real densities of the species in the floor.

Notwithstanding it seems probable that with frost *Dendrobaena*, Staphylinidae — larvae and imagines — and Cantharidae larvae withdraw into the lower layers of the floor (H and A₁) : during the period of frost the catches in these layers are higher than in the upper layers, whereas the density in the H layer during January is higher than in November-December and March as seems from comparison of the results of these months with those of 20th January. This comparison is admissible as the samples of the last date were not thawed artificially.

This withdrawal into the lower layers may also apply to *Cylindrojulus* and *Araneina* though these data are less clear. The Entomobryomorpha do not move into the lower layers but chiefly remain in the F layer. Incurvariidae, *Phaenocladus*, Anthomyidae and probably *Acrotrichis* behave likewise. *Athous* and *Rhagio*, having normally their optimum in the lower layers, remain there in winter.

2 Phenology and Development

From the data as they are summarized in Table C (appendix) it is possible to get an insight into the cycle of life of several species.

If the smallest animals are caught only during a short part of the year it is clear that the eggs were laid during a certain period (the incubation period) before the appearance of the youngest animals.

This is most obvious for Cantharidae, *Athous* and *Rhagio*, which lay their eggs in summer and for *Phaenocladus* and Anthomyidae, which reproduce in autumn. It seems from the data that *Dendrobaena* only laid eggs in autumn. Of *Arion*, Geophilidae and *Cy-*

lindrojlulus the youngest animals are caught during the whole year. In these animals reproduction takes place during a great part of the year or at least in more than one period. The often small number in which the youngest animals in all groups are caught is partly to be attributed to the desiccation technique, which is undoubtedly less reliable for the smaller animals than for the bigger ones.

Whether the development of larvae of beetles and flies takes one or more years is also clear from this table.

For larvae developing into imago within a year we find during the period that the youngest animals occur no halfgrown larvae and at best a very small number of full-grown larvae in comparison with the preceding part of the year. *Rhagio lineola* is a clear example of a species with a duration of development of one year. The other fly larvae too, *Phaenocladus* and Anthomyidae, appear to develop within a year.

A time of development of more than one year is shown by Cantharidae and *Athous*. For both species we find the youngest instars at the same time with the larvae that are still far from full-grown. The full-grown instars of Cantharidae (about 15 mm) only appear in the samples of winter. The intermediate instars occur during the whole year. So this species has a development of at least two years. The size of the larvae after one year and the size of the full-grown larvae lead us to suppose that the larvae attain maturity and pupate in the third winter after their birth. Data from literature affirm this supposition (ESCHERICH 1923).

The full-grown larvae of *Athous* too, we only find in the winter samples. The great difference in length between larvae of one year old and full-grown larvae makes it likely that the development of these larvae takes at least three years but probably still more.

b Special Part

In the following discussion of the hemiedaphic macrofauna nomenclature is according to the identification keys used mentioned separately at the end of the list of references (p. 167). The following figure and tables have to be referred to: fig. 12 (vertical dispersal), table B (horizontal and vertical dispersal), table C (phenology) and table 16 (vertical dispersal of separate size classes).

ANNELIDA — OLIGOCHAETA

Enchytraeidae. The desiccation method is not reliable for this group of animals. In the first place even slow desiccation of the samples is harmful for these animals with their very thin cuticula. Besides, there also remain animals on the walls of the funnel and desiccate there.

The real density is no doubt considerably higher than appears from the results presented here (table B, appendix), it is probably about some thousands per m². This is affirmed by the catches from the samples of 40 cm³ of January 1947. In applying the immersing

technique (table 15) a density of 10,000—25,000 per m² could be calculated for the H layer. Taking the unsuitability of the method into account, the numbers in table B point to a dense population of enchytraeids, especially in the layer of leaves newly fallen in autumn.

The inadequacy of the method for a quantitative investigation and the difficulty of identifying the species made us abandon a further investigation of this group. No doubt they are important in decomposing the litter and it will be of much value to investigate this group thoroughly. FORSSLUND (1943) e.g. informs that they are able to form amorphous humus from humus little decomposed, and already in 1920 JEGEN proved in breeding tests the important part these animals play in decomposing organic material. He also proved that they can be of great influence as enemies of parasitic nematodes in agricultural soils.

Lumbricidae. *Dendrobaena octaedra* Sav. and *Lumbricus rubellus* Hofm. are the only lumbricids that were caught. Both are chiefly met with in the litter layer, less in the H layer and very rarely in the sand layer. With severe frost *Dendrobaena* was most numerous in the H layer. There is no question of digging canals into the soil and pulling down litter as is known of other lumbricids.

Dendrobaena octaedra chiefly feeds on litter of the F layer, of which only the nerves and stalks are left. The excrements, irregular grains of 2—5 mm, consist for the greater part of very small fragments of litter (15—150 μ). Larger parts of leaves are also found. The whole is interwoven by numerous mould hyphae, already present in fresh excrements, which must consequently have passed the intestinal canal unaffected. The excrements are put down between the leaves and mostly contain only few sand grains. Evidently these worms contribute considerably to the decomposition of the litter. F₀ litter is only little eaten by *Dendrobaena*. Five specimens ate only 25 mg (air-dry) of this material in three weeks under standard culture circumstances: temperature of the room (18—20° C) and 70 % water content. Of material from the F₁ layer 265 mg was turned into excrements in the same circumstances. Of F_x material probably a much greater quantity would be consumed. It is, however, practically impossible to separate food material and excrements in this case, so that no data are available.

From the summarizing table C (appendix) it appears that young specimens of ± 10 mm only occur in autumn. According to these statements it may be supposed that the eggs are deposited only in autumn. Data are insufficient, however, to conclude this with certainty, the more so as EVAS and MCL GUILD (1948) found that under natural conditions of soil temperature, but at optimum soil moisture all species investigated by them reproduce throughout the year.

From the density per 4 dm³ in the separate litter layers a density of 30 specimens was calculated for a surface of 1 m² with layers of average thickness. In Denmark *Dendrobaena octaedra* is

also the only species occurring in raw humus. It is here about 10 % of the weight of all animals (BORNEBUSCH 1930).

Lumbricus rubellus Hofm. was only so rarely found that it is left out of consideration here.

MOLLUSCA — PULMONATA

The only mollusc regularly caught in the samples of 4 dm³ was the slug *Arion subfuscus* Drap. This species was caught throughout the year. It was absent in the samples of the severe winter of 1947. In the samples of March following this winter it did not occur and during the spring it was also less observed than in the spring of 1946. So it is probable that this slug suffered much from the extreme circumstances.

This species has its optimum, as might be expected, in the F₀ layer in which it occurs with an average density of 2.6 per 4 dm³. The average density per 1 m² amounts to 14.

Next to rare catches of *Arion intermedius* Nor. and *Limax tenellus* Nil. a very small *Hyalinia* sp. was caught in a small number. Though the catching method was not suitable for the latter, the catches were not only so small for this reason. During the whole working period it was only very seldom observed.

ARTHROPODA — ISOPODA

Isopoda were scarcely represented in the litter layer examined. In total only some specimens of the species *Porcellio scaber* Latr. and *Phylloscia muscorum* Scop. were caught.

They are litter eaters, but of little importance in the forest examined.

CHILOPODA

The group of the centipedes occurring most numerous in the considered floor is the order of the Geophilomorpha represented by two species viz. *Brachygeophilus truncorum* Mein. and *Schendyla nemorensis* Koch. Unfortunately, these two species were not separated at the countings and were taken together as Geophilidae in the tables. The following notes concern the two species together.

These animals have their greatest density in the humus layer and in the upper sand layer. Striking are the great numbers, repeatedly occurring per sample, from which it appears that the species often occurs in "colonies". These are composed of animals of varying lengths so that the idea must be excluded that the colonies are communities of young animals originating from eggs of one or more animals, deposited on a favourable place. The concentrations may be explained by locally favourable circumstances or by social instincts. Experiments are needed for the explanation of this phenomenon.

In consequence of the varying density the figures on the vertical dispersal are highly influenced by accident. It is, however, certain that they have their optimum in the lower litter layers. The density per m² of an average composition was calculated on 172 specimens.

It is clear that, owing to the irregular dispersal, this number does not mean any more than a datum to fix the order of magnitude. All sizes occurred during the whole year.

Geophilidae seem to feed both carnivorously and phytophagously (BRADE BIRKS 1929).

Of the other Chilopoda, present in this forest soil, *Lithobius calcaratus* Koch and *Lithobius forficatus* L. were caught though in much smaller numbers. The density of the former, the more abundant of the two, was 7 per m². The vertical dispersal was fairly regular in all layers. *Lithobius forficatus* was mostly found in tree-stumps or under stones and trunks.

Observations and examinations of stomach contents (referred to by BRADE BIRKS 1929) made it certain that the *Lithobius* species exclusively feed carnivorously.

DIPLOPODA

The millipedes are represented by two species only, both belonging to the family of the Julidae: *Cylindrojulus silvarum* (Mein.) and *Julus scandinavicus* Latz. In counting, the two species were not distinguished. By far the greater part of the animals belonged to the former species, so the following details apply to *Cylindrojulus silvarum* and are only to a small degree confused by the included specimens of the other species.

The vertical dispersal (fig. 12) shows that these animals occur with the greatest density in the lower layers of the floor (about 10 per 4 dm³ H). This is connected with food requirements of these species: own breeding tests proved that neither of the species eat the newly fallen leaves.

In spring (the middle of March — the middle of May) the two species were caught at night in catching boxes in rather large numbers (see fig. 14). This great mobility overnight in spring was also fixed by BRADE BIRKS (1922) in Kent for several species and was qualified by him as migration movements. Exact observations will, however, have to affirm this. Possibly this mobility is to be ascribed to reproduction activity in our case. Copulations were regularly observed in spring but they also took place in June and autumn when nothing was noticed of such mobility.

As seems from table C (appendix) all classes of size except class I occur during the whole year. That the first class was not present in winter and spring samples of 1946 must be accounted to accident: from January up to March 1947 it was present in several samples. So it is probable that eggs are laid during a long period of the year, which agrees with the observation of copulations on different times of the year.

According to VERHOEFF (1932) the eggs of Julidae are laid in large numbers in a sort of nest in the soil. The first two stages only take some days for their development, afterwards the development is much slower.

Cylindrojulus silvarum, like the species examined by VERHOEFF,

Table 19. Some characteristics of the different instars of *Cylindrojulus silvarum*.

Instar	number of legs	number of segments	length in mm.
I	3	8	2
II	7	12	2 $\frac{1}{2}$, 3
III	17	19	3 $\frac{1}{2}$, 4
IV	31	24, 26	4 $\frac{1}{2}$, 5
V	41, 43	30, 31	6 $\frac{1}{2}$
VI	55	39	10, 10 $\frac{1}{2}$
VII	69	43, 44	12, 14

has at least 7 larval instars, distinguished among other things by the number of legs and segments and the length. Table 19 gives a survey of the characteristics in the different stages fixed at a rather small number of animals. The number of legs and segments may vary much for the older larval stages and for adults: females are much larger and have greater numbers of legs and segments than males. Also in maturity animals still moult repeatedly.

Little is known about duration of the development of millipedes. VERHOEFF (1932) concluded to a time of development from egg to maturity of 1 $\frac{3}{4}$ year for *Tachypodojulus albipes* Koch. Our breeding tests of *Cylindrojulus silvarum*, though not continued for such a long time, also point, to a slow growth (see table 20). In these cultures, beginning on 5th September 1947 three groups of ten animals measuring resp. 6-8, 8-10 and 15-20 mm were bred both on F₀ and F₁ layer of beeches under standard conditions: temperature 18-20° C, 70% water content. The first months the development on F₀ shows only little difference with that on F₁ though less of the F₀ litter was eaten. Then the increase of weight of the larvae on F₀ gets considerably smaller and after that a very great mortality occurs, first among the oldest animals. In the F₁ tests the youngest animals develop most quickly, the oldest ones slowest. After 8 months the youngest animals have gained 600% of their original weight, the older 320% and the oldest 40%.

From the numbers of specimens in which the different classes of size are caught during the year 1946 (table 16) it seems that the densities of the classes II (4-8 mm), III (8-16 mm) and IV (> 16 mm) decrease in this order in spite of the fact that the rapidity of growth is smaller in the older larval stages than in the younger ones. Application of the test of SWED and EISENHART (1943) to the series of numbers in the H layer gives significant differences for the series of each class. For the classes II and III $P = 0.023$, for the classes III and IV $P = 0.003$, indicating that the differences may occur as a consequence of accident only with a probability of respectively 23 and 3 on 1000 cases. These differences in numbers might be explained by a temporarily increasing reproduction or because the possibility of development gets more favourable for the larvae. These explanations are thought improbable. On other areas in preceding years larvae of the second class were caught too in larger numbers than the third class and the latter

Table 20. Development of *Cylindrojulus silvarum* on beech litter of different age.

Date	Reared on newly fallen beech litter (F_0)			Reared on several years' old beech litter (F_x)		
	Number	Length in mm	Average weight in mg	Number	Length in mm	Average weight in mg
5 IX '47	10	6—8	2.8	10	6—8	2.6
30 X '47	9	7—9		9	7—8	
11 XII '47	8	8—10	5.0	7	8—10	5.4
3 II '48	8	9—11	8.0	6	10—12	9.2
22 III '48	7	10—13	9.3	6	11—15	13.9
12 V '48	7	10—13	9.1	6	12—18	18.2
25 VI '48	5	11—13	8.2	5	16—18	20.8
9 VIII '48	3	11—13	10.7	5	16—18	21.4
5 IX '47	10	8—10	5.5	10	8—10	5.5
30 X '47	10	10—11		7	10—11	
11 XII '47	9	11—13	9.6	7	11—13	9.4
3 II '48	9	12—13	10.6	6	15—16	17.4
22 III '48	9	12—15	11.9	6	15—17	18.3
12 V '48	1	12		6	17—19	23.2
25 VI '48	—			6	17—20	25.3
9 VIII '48	—			6	17—20	25.3
5 IX '47	10	15—20	24.1	10	15—20	24.6
30 X '47	9	17—20		9	16—20	
11 XII '47	6	17—20	29.3	8	18—21	28.0
3 II '48	6	17—20	30.2	7	18—21	30.4
22 III '48	3	19—20		6	19—21	31.8
12 V '48	2	20		6	20—22	34.2
25 VI '48	1	19		5	20—23	39.0
9 VIII '48	—			3	20—23	47.3

in larger quantities than the fourth class. Besides, the population density in 1945 was, as far as observed not perceptibly lower than in 1946. It seems more probable that the differences in the densities of the different classes of size should be attributed to mortality.

This can be caused by several factors. Little is known of predators in consequence of the hidden way of living. During moulting the animals burrow themselves into the sand layer (VERHOEFF l.c.), in which way they are protected against an attack of predators in these vulnerable stages. Moreover, millipedes are protected against many enemies by the poisons excreted on both sides of each segment. Still repeatedly carabids and staphylinids were observed devouring a millipede, so it is probable that these preying beetles levy a toll of these animals. The significance of endoparasites, of which Gregarina and Nematoda must be mentioned, and that of ectoparasites, moulds and mites, as factors in causing mortality, is unknown. These factors as good as climatic and edaphic factors as causes for mortality have to be studied in detail before something is to say about the causes of the stated mortality. A great difficulty in these studies will be the slow development of the species.

As appears from breeding tests, which will be discussed in chapter

VI, millipedes may yield an important contribution to the decomposition of the forest litter. No doubt, the influence of *Cylindrojulus silvarum* in the forest investigated (average density 80 ind. per m²) will be rather important. The difficulties in ascertaining the exact contribution of any saprophagous species to the litter decomposition in the forest investigated will be discussed too in chapter VI.

In literature several cases are mentioned with respect to the influence of millipedes on the decomposition of litter. COLVILLE (1913) records about a very large species *Spirobolus marginatus*—about 7 cm long—from Washington, which was caught in 320 specimens on a surface of 1.20 × 6 m. Everywhere their activity was shown by large amounts of excrements. One animal produced in captivity 1/2 cm³ excrements per day. ROMELL (1935) described the influence of two *Fontaria* species on the formation of mull in a forest on the Adirondack Mountains. Next to litter the animals ate moulds, but newly fallen litter was despised. The excrements were mixed with mineral substrate.

In connection with the importance of millipedes for decomposition of organic material it may be mentioned that several cases are known of wholesale development of millipedes.

A wholesale occurrence of millipedes in Europe was reported by PAZLAVESKY (1879) in Hungary and Transsylvania, and by VERHOEFF (1900) in the Alsace. In America wholesale increases of species of *Fontaria* were reported by MAUCK (1901) and BROOKS (1919). In contrast to the records from Europe, which always deal with species of open areas, those from America concern species that normally occur in woods, strongly increase there and afterwards spread outside the woods in enormous numbers. From a theoretical point of view, in forests with a thin litter layer the favourable influence of the litter cover may be destroyed by the activity of a great number of millipedes (BRADY BIRKS 1930). Nothing is said about this in the cases mentioned above.

SYMPHYLA

Of the other Myriopoda only *Scutigera immaculata* Newp. was sometimes caught in very large numbers, chiefly in the upper sand layer, when this was mixed with some humus. The numbers are too irregular (from 0-200 per 4 dm³) and the number of samples is too small to give the average density. The animals—about 2 mm in length—are generally considered saprophagous. In the forest investigated they are presumed to be of local importance.

INSECTA

The insects have a very great number of representatives in the litter layer, both in respect of the number of species and of the number of specimens.

The groups discussed above spend their whole cycle of life in the soil or are at least able to do so: geobionts.

Some groups of the insects also belong to the geobionts: Diplu-

ra, Protura, many species of the Collembola and a number of the Coleoptera spend their whole life in or on the forest floor. The greater part of the soil insects, however, belongs to the geophiles. Many of them only spend their earliest stages in it: Diptera, a number of Lepidoptera and many Coleoptera. Others only stay there during a period of rest, either as cocoon (some Lepidoptera and Hymenoptera) or as imago (several Rhynchota and Coleoptera). Especially the group of geophiles mentioned first, the insect larvae, may be of great importance in the community of the soil.

Just as in the other groups, only those insects are dealt with that occur in such a large density that they are regularly found in the samples of 4 dm³. For this reason some orders, though having several representatives in the fauna of the soil, are not mentioned here.

DIPLURA

The only representative of this order is *Campodea staphylinus* Westw. This species has its optimum in the two lower layers of the floor: the humus layer and the upper sand layer. The average density of this little species — with a length of 2-4 mm — was calculated at about 200 per m². Because of its omnivorous habit of feeding (HANDSCHIN 1940) this species may be of some importance in the decomposition of the litter.

PROTURA

The only representative of this order was identified as *Acerentomon doderoi* Silv. It is completely absent in the litter of beeches. Only in the most N.W. part of the forest where only oaks grow, it occurred in large numbers (up to several hundreds per m²). About the way of living nothing is known with certainty.

COLLEMBOLA

Next to some *Entomobrya* species, occurring in a very small density, the greater Collembola were represented by the species *Lepidocyrtus lanuginosus* (Gmel.), *Tomocerus flavescens* Tullb. and *Tomocerus longicornis* (Müll.). They are by far the most numerous in the upper litter layers where they feed on moulds and litter as can be deduced from the intestinal contents. No doubt these species will vary in number in the course of the year. To trace these fluctuations in detail it will be necessary to take the samples in greater numbers and frequency than was done here. The average density was calculated at about 100 per m², a very small value, that is only partly to be explained by the escape of animals in sampling and sieving. The F_x samples of 40 cm³, taken in the same year give an average of 0.6 per 40 cm³ = 60 per 4 dm³ whereas in the samples of 4 dm³ in the same layer an average of only 2.5 was found. These values differ too much to be explained from local differences in the forest. In my opinion the most important causes of mistakes are:

1. The fact that part of the animals remain unobserved in the catching often dirtied rather much.

2. The fact that these small animals die during desiccation of the relatively thick sample layer in the Tullgren-apparatus.

This group as well as the Symphyla, the Diplura, the Protura and the little Diptera larvae will be collected best in samples between 40 cm³ and 4 dm³, e.g. 400 cm³.

The Symphypleona were only present in very small numbers of individuals in the forest investigated. This is to be expected since any herbaceous vegetation is absent here: the majority of the species of this group inhabits the herbaceous layer and only strays into the litter layer (AGRELL 1941).

RHYNCHOTA

Next to bugs, leafhoppers and aphids, occasionally present on or in the litter layer, only during the winter halfyear hibernating imagines of the Pentatomidae were regularly caught. The following species were identified by Dr H. C. BLÖTE: *Elasmucha grisea* (L.), *Elasmucha picicolor* (Westw.), *Elasmotethus interstinctus* (L.) and *Acanthosoma haemorrhoidalis* (L.). They chiefly inhabited the lowest litter layer. Their total average density amounted to 9 per m² during the period from August to April.

COLEOPTERA

Among the beetles are both geobiontic and geophilous species. Of the first group only the Staphylinidae and the Ptiliidae are discussed here. The other geobiontic families (a.o. Carabidae, Silphidae and Scarabaeidae) were caught in very small numbers. Of the geophiles spending their developmental stages in the soil the most important representatives are: Elateridae, Cantharidae, Tenebrionidae and Curculionidae.

Staphylinidae. The small representatives of this family occur in a sufficiently large density to be examined in samples of 4 dm³. Both larvae and imagines occur in all layers. That the greatest average density of the adults occur in the F layer is to be ascribed to the very high catches in this layer in November and December, the cause of which is unknown. Larvae and imagines were caught throughout the year. How far this can be applied to each species separately was not decided in consequence of the lack of keys for identification of the larvae and the difficulties in rearing them.

The material (adults) of November and December 1946 was identified by Mr. W. C. BOELENS. Table 21 gives the numbers in which the different species were found in the samples. Three species seem to dominate: *Oxypoda annularis* Mannh., *Sipalia circellaris* Grav. and *Atheta fungi* Grav. Also *Othius myrmecophilus* Kiesw. and *Mycetoporus clavicornus* Steph. have a somewhat larger density.

Little is known about the exact feeding habits of these animals. RENKONEN (1948) found by analysing the contents of the intestines

Table 21. Staphylinidae in the floor of the beech forest 8 G.

	Different data 1946 F samples	19 XI 1946		5 XII 1946	13 XII 1946	
		4dm ³ F (1)	4dm ³ F (2)	4 × 4 dm ³ F ₀	4dm ³ F (1)	4dm ³ F (2)
<i>Oxyptoda annularis</i> Mannh.	1	1	19	1	8	3
<i>Sipalia circellaris</i> Grav.	17	9	26	2	6	12
<i>Atheta fungi</i> Grav.	17	8	6	14	40	26
<i>A. gagatina</i> Baudi		1				
<i>A. gregaria</i> Er.		1				
<i>A. palustris</i> Kiesw.	1					
<i>A. nigrifula</i> Grav.			1			
<i>Habrocerus capillaricornis</i> Grav.		1			1	1
<i>Mycetoporus clavicornis</i> Steph.	8	2	4			1
<i>M. splendidus</i> Grav.	3					
<i>Othius myrmecophilus</i> Kiesw.	5	2	2		5	2
<i>O. punctulatus</i> Goeze	2	1			3	
<i>Xantholinus linearis</i> Oliv.		1				1
<i>Olophrum piceum</i> Gyll.	1			4		
<i>Lathrimaeum atrocephalum</i> Gyll.	3			4		
<i>Acidota crenata</i> Mannh.	1		2			
<i>Proteinus brachypterus</i> F.				2	1	

that most Oxytelinae feed on plant material, chitin parts were not observed. However, this does not exclude the possibility of animal food.

Densities of 108 and 116 per m² on an average were calculated for larvae and imagines respectively. Collectively these species will take a rather important place in the litter community.

Ptiliidae. Of these geobiontic beetles the very small *Acrotrichis* spec. must be mentioned. It has its largest density in the F layer where it was very numerous, especially in autumn.

The average density was estimated to be about 70 per m². With respect to the size (< 2 mm) it is not probable that this species plays an important part in the litter community in this density.

Elateridae. The wireworms were represented by one species only in the forest investigated: *Athous subfuscus* Müll. Sporadically also *Dolopius marginatus* L. was found. In the adjoining oak and spruce woods it was, however, as numerous as *Athous* was there. Further *Melanotus rufipes* Herbst. was stated in low numbers; this species especially occurred in half-mouldered tree stumps.

Table C shows that the first larval stage of *Athous subfuscus* (< 2 mm) was only caught in August. In 4 of 10 F_x samples of 40 cm³ taken on 30 VII 1946 respectively 11, 3, 2 and 1 larvae < 2 mm were found. The eggs were apparently laid in groups from which the young animals disperse rather quickly. The development of the young larvae is slow. In a test made by Dr ROOSEBOOM

a larva reared on beech litter and humus moulted only twice in 14 months : in the first moulting it grew from 5 to 10 mm, in the second from 10 to 15 mm. The animal lived quite saprophagously during this period and turned a good deal of feeding material into excrements. This slow development agrees with what is known about wireworms noxious to agriculture (mainly *Agriotes* species) which moult nine times during five years of development (EVANS 1944).

All stages have their optimum in the H layer, where they chiefly feed on material in an advanced stage of decomposition and perhaps on roots of trees. This species, like other wireworm species, may be noxious by eating seeds of trees. v. BUTOVITCH (1933) and SCHAEFFENBERG (1942) call it omnivorous as it eats in captivity also pupae of Geometrid moths and pupae of weevils. BORNEBUSCH (1930) did not succeed in making them prey on *Diprion* cocoons but he stated that they entered into the cocoon when the sawfly has left it and supposes that they eat the remnants of the pupa here.

The average density was 218 per m². *Athous subfuscus* is likely to play an important part in the decomposition of the litter with this density.

Cantharidae. These beetle larvae live of preying and have their optimum in the lower litter layers. The smallest larvae were only caught in August and October, the largest in autumn, winter and spring, the two intermediate classes throughout the year. In accordance with ESCHERICH (1923) it may be concluded from these facts that the larvae are full-grown and pupate in the second spring after their birth. It is to remark that in spring full-grown larvae are regularly caught in catching boxes (increased mobility before pupation?).

Rearing these predacious animals failed and no imagines could be got from the larvae. It is quite certain, however, that all individuals belonged to one species, most probably a *Cantharis* species. It appears from table C that the numbers of the animals in the higher classes of size decrease much. No doubt many of the numerous young larvae fall a prey to other predators.

The average density of this species is 103 per m². It may be of some importance in the forest investigated.

Tenebrionidae. Both larvae and imagines of *Helops laevis* Goeze were rather regularly found in the samples, especially in the S.W. part of the forest, where the floor is more solid than in the rest. Often larvae and imagines were found in twigs, partly eaten out and for the greater part filled with excrements of these animals. Though the number of larvae caught was too small to calculate the density, it may be estimated 2.5 per m² in the S.W. part.

Curculionidae. *Ceutorhynchus* spec., *Strophosomus rufipes* Steph. and *Strophosomus melanogrammus* Först. were caught regularly, the latter in the smallest numbers. Though these species are supposed to stay in the soil for a long time, they do

not belong to the geobionts: *Ceutorhynchus* was not caught in the summer months, *Strophosomus* spec. inhabits the trees they feed on during a great part of the year.

The larvae of *Strophosomus* were regularly found in the mineral soil where they feed on roots.

HYMENOPTERA

The ants are the most important representatives of this order in the floor fauna. In their investigation into the dispersion of the ants' fauna both QUISPEL (1941) and WESTHOFF et al. (1943) concluded to a small density of *Myrmica ruginodis* Nyl. in beech forests without undergrowth. Their experiences were entirely confirmed in the beech forest investigated. In the 4 dm³ samples only seldom an individual of this species was found, whereas the other species failed completely. In a direct examination of 5 surfaces of 10×1 m throughout the forest 3 nests of *Myrmica ruginodis* were found in the S.W. part, distinguished from the rest by a more solid humus layer. It is possible that in this part of the forest the temperature in the floor is somewhat more favourable than in the other part: the litter is only very thin here in contrast with the rest of the forest. That the solid structure is of importance is not thought probable as the density of this species can be very high in oak forests with a floor of a loose structure.

The importance of the ants in the community investigated is undoubtedly very small.

DIPTERA

A great number of Diptera spend their larval stage in the litter layers of the forest: they belong to the geophile animals. Of these Diptera larvae the following families were caught numerously, though sometimes only during a short time.

Bibionidae. The larvae caught are supposed to belong partly to the species *Bibio hortulanus* L. var. *Marci* L. for of this species the imagines were seen in great numbers in April and May. At oviposition many eggs are laid on the same spot, for which reason the larvae also occur in large groups. Still, separate larvae were also often caught so that the appearance in groups is certainly not obligatory in this family.

In 1946 the density of this species was small: next to some catches of 1-3 individuals per 4 dm³ larger numbers were only caught in two samples, viz. 26 and 105 specimens.

ESCHERICH (1942) mentions some cases of wholesale occurrence of the larva e.g. in an unmixed spruce forest in which the groups of larvae were found all over the forest. These groups consisted of thousands of animals occupying a surface of about $\frac{1}{4}$ m². HOFMANN (1937) emphasized the importance of these larvae for the decomposition of organic material.

Sometimes damage seems to be done by specimens eating living roots of trees (ESCHERICH 1942). Compared to their great influence

on the decomposition of the litter this may be, however, of little importance.

Mycetophilidae. Most *Mycetophilidae* live in toadstools. Some of them also live saprophagously in the litter layer. Mostly they were caught in small numbers in a sample (up to 10 per 4 dm³). It is supposed that part of the delicate animals die in the desiccation process. So the numbers found do not give a correct impression of the real density. Compared with the numbers found of the next group the density of this group was undoubtedly much lower.

Lycoriidae (= *Sciaridae*). The most important representative of this family found in the forest investigated is *Lycoria sociata* Win. In the spring of 1946 the young larvae of this species were found in groups regularly spread all over the forest. The number of larvae in a group ranged from some hundreds to some thousands. The larvae were also found in the adjoining oak forests and in other beech forests in the environment. In the beginning of May the larvae were full-grown (length about 10 mm), they pupated in the middle of May and the imagines appeared at the end of May. Because of their short time of life (only some days) and their long hatching period the small midges were hardly observed in the field. In the middle of July and in November again rather large numbers of larvae were observed in groups of some hundreds. In the spring of 1947, they were still sporadically found. The suddenly wholesale appearance of this larvae makes one think of the appearance of army worms, large troops of larvae, slowly moving at regular intervals. This is known of several species like *Lycoria militaris* Now., *Lycoria thomae* L. and *Semisciara agminis* Kjell. (KJELLANDER 1943). Of *Lycoria sociata* no migration was observed by me. Still the group is able to move over small distances, as the places where the lower litter layer was eaten away were much larger than the room occupied by the larvae. Even a long time after the hatching of the adults the traces were still distinctly recognizable by the absence of the lower litter layers and the presence of black fine-grained masses of excrements. Because of the large number of individuals in which the species may appear, it is, no doubt, of great importance in decomposing the litter. The circumstances leading to a wholesale development are, however, not yet known.

Chironomidae (= *Tendipedidae*). The only genus of this family, regularly found in the floor was *Phaenocladus*, the small larvae of which were rather numerous in the upper litter layer during the winter half-year. Its average density was 17 individuals per 4 dm³ in the period from December-May and its density per m² of the whole floor proved to be 50. For these small animals this is certainly too small a density to credit them an important part in the decomposition of the litter. As in the preceding groups of midge larvae this is, however, a minimum value, as part of the small delicate larvae is supposed to die during desiccation.

Cecidomyiidae (= *Itonididae*). A great part of the gall midges does not cause galls, but lay their eggs in decomposing parts of plants in which the larvae feed saprophagously or carnivorously. These small larvae (1—3 mm) occur in large numbers (up to some hundreds) in the samples of 4 dm³. Probably these numbers are relatively still higher in smaller samples (see p. 113). According to the different ways of living the larvae of this family constitute a heterogeneous group in ecological respect. So an estimation of the total density of this group is of no value. An investigation with samples of an adequate size and breeding tests with larvae will throw light upon the importance of this family.

Of the other families of the *Nematocera* only small numbers of larvae were caught.

Of the *Tipulidae* the species *Tipula scripta* Mg. was regularly caught. In a large density this species may be of much importance for the decomposition of the litter. Rearing on beech litter gave a good development of the larvae, like rearing on the litter of oaks, pines and even larches.

Larvae of *Limnobiidae*, *Scatopsidae* and *Ceratopogonidae* were only sporadically found. According to literature they also live saprophagously but in the density stated they cannot play an important part in the decomposition of the litter in the forest investigated.

Rhagionidae (= *Leptidae*). *Rhagio lineola* F., the only representative of this family in our material, was regularly found. It had its highest density in H and A₁ layer (resp. 5.3 and 5.0 ind. per 4 dm³). It appears from table C that the species has a development of one year. Adults were common in the summer months in accordance with the appearance of larvae of the first instar. According to literature the larvae feed predatorily. The average density on 1 m² of the floor was calculated at 58.

Dolichopodidae — *Empididae*. It was not possible for me to distinguish the larvae of these two families, nor did I succeed, in spite of several attempts, in rearing the larvae into imagines. On account of morphological differences it may be said that at least four species occurred. From November to June they were frequently caught up to some tens per sample of 4 dm³. The smallest specimens (2—4 mm) were caught in autumn and winter, the largest (4—8 mm) in spring. This points to a life cycle of one year. According to literature these larvae have predatory feeding habits.

Syrphidae and *Asilidae*, also predatory fly larvae were fairly frequently caught but in so small numbers that they will be only of secondary importance in the community investigated.

Anthomyidae. The larvae of the families of the *Schizophora* are still very insufficiently known and the majority is not to be identified in consequence of their great similarity. The genus of

Fannia is an exception because of its typical form. *Fannia* larvae were met with in a small density throughout the year. In summer their number was very small, the smallest animals were caught in autumn. Their average density was greatest in the F layer and amounted to 8 per m². The habit of feeding of these larvae is, in accordance with literature, supposed to be mainly saprophagous.

The larva of another species of Anthomyidae (indicated in the tables by Anthomyidae) was very numerous especially in the F₀ layer from November to March. In this period a distinct growth was seen from 2 to 7 mm. This species too lives mainly saprophagously. Its preference for the F₀ layer is remarkable since no other species prefers this layer. The short term of development during a time that this layer does not desiccate (autumn, winter) makes this possible. The average density was 37.8 per 4 dm³ in this period, and the average number per m² was calculated at 131 individuals. This species may be of some importance.

LEPIDOPTERA

Of this order only the larvae of species developing in the litter were caught. In the desiccation process pupae of these species and also pupae of species spending only pupation stage in the floor remain in the samples to a great extent. However, larvae as active organisms are of greater importance in the community of the litter than pupae, which only increase the food supply of the larger predators and parasitoids. In the beech forest investigated small numbers of cut-worms (*Agrotis* spec.) were caught.

More numerous were the larvae of Incurvariidae, which mine in living leaves as young larvae and afterwards live in the floor, between two pieces of dead leaf cut out sacciformly. They feed chiefly on litter material. Most numerous was the species *Adela viridella* Sc., the imago of which flies in April and May. The larvae have the greatest density in the lower litter layers (5 ind. per 4 dm³). Their average density per m² was 19.

ARACHNOIDEA — CHERNETES (PSEUDOSCORPIONES)

The false scorpions are represented by one species: *Obisium muscorum* Leach. These small predators (maximally 4 mm long) occur especially in the upper litter layers and fail in the sand layer. The average density was calculated at 8 per m². In this density these animals cannot have an important rôle in the community.

OPILIONES

For these relatively large animals the samples were too small to catch sufficient numbers for estimating their density. Moreover, the litter layer is but part of the habitat of most species: they are also found in the herbaceous layer and even in the tree layer.

Of the six species that were caught the following occurred in largest numbers:

Oligolophus tridens (Koch), reaching maturity not before autumn,

Platybunus triangularis (Herbst.), mature in early summer and disappearing in July,
Nemastoma lugubre (Müll.), a true geobiontic species, after *O. tridens* the most numerous species.

In low numbers were caught: *Liobunum rotundum* Latr., *Phalangium opilio* L. and *Mitopus morio* Fabr.

ARANEINA

By far the most numerous group of the macro-Arachnoidea are the spiders which occur in diverging sizes. The largest animals do not lend themselves to a quantitative investigation by means of samples of 4 dm³ because of their small density. The species moving at the surface are caught in the catching boxes in large numbers.

The following floor inhabiting species were identified by Drs L. VAN DER HAMMEN:

<i>Hahn timer helveola</i>	Simon	(Agelenidae)
<i>Hahn timer ononidum</i>	Simon	"
<i>Robertus lividus</i>	(Blk.)	(Theridiidae)
<i>Lepht hyphantes flavipes</i>	(Bös.)	(Linyphiidae)
<i>Lepht hyphantes</i>	spec.	"
<i>Microneta viaria</i>	(Blk.)	"
<i>Macrargus rufus</i>	(Wid.)	"
<i>Centromerus silvaticus</i>	(Blk.)	"
<i>Centromerus dilutis</i>	(Cambr.)	"
<i>Wideria cucullata</i>	(Koch)	(Micryphantidae)
<i>Trachynella obtusa</i>	(Blk.)	"
<i>Haplodrassus silvestris</i>	(Blk.)	(Gnaphosidae)
<i>Agroeca brunnea</i>	(Blk.)	(Clubionidae)
<i>Lycosa chelata</i>	(Müll.)	(Lycosidae)
<i>Lycosa</i>	spec.	"
<i>Trochosa terricola</i>	Thor.	"

In addition the following species were met with hibernating or as casual guests:

<i>Anyphaena accentuata</i>	(Wlk.)	(Anyphaenidae)
<i>Clubiona holosericea</i>	(L.)	(Clubionidae)
<i>Clubiona brevipes</i>	(Blk.)	"
<i>Clubiona</i>	spec.	"
<i>Aranea cucurbitina</i>	L.	(Argiopidae)
<i>Meta reticulata</i>	(L.)	"

Of these species *Hahn timer helveola*, a small spider of about 2 mm, was the most numerous. It has its largest density in the H layer, in which it was found to a maximum of 20 individuals per 4 dm³. After *Hahn timer*, the small Linyphiidae and Micryphantidae were most numerous. They had their optimum in the lower F layers.

The average density of all spiders per m² was calculated at 125 for the smallest species (>2 mm), 98 for the spiders from 2—4 mm, 8 for spiders from 4—8 mm and only 1 for spiders still larger. The densities in which the different sizes occur lead to suppose that spiders have rather great influence on the composition of this community.

D. EPEDAPHIC MACROFAUNA

Under this heading all macroarthropods are summarized that move over the forest floor and for that reason could be caught in tins dug in the soil. As we saw already in discussing the catching technique the most important animals of this group are: beetles (Carabidae, Silphidae, large Staphylinidae, Scarabaeidae, Tenebrionidae), a number of spiders (Lycosidae, Linyphiidae, some Clubionidae) and harvesters (Phalangidae). Moreover, individuals of the following families and orders were caught in the boxes in small numbers: Julidae, Orthoptera, Rhynchota, Elateridae adults, Cantharidae larvae, Tipulidae larvae and *Agrotis* larvae.

In chapter III it was explained in which manner and at which time the density of the species caught in large numbers was determined by means of the Lincoln-index. In addition to the density, which could only be determined for some species, the catching results yield an insight into the following questions: 1. The horizontal dispersal of the species over the experimental plot. 2. The day and night activity of the different species. 3. Phenology and seasonal fluctuation.

a. General Part

1. Horizontal Dispersal

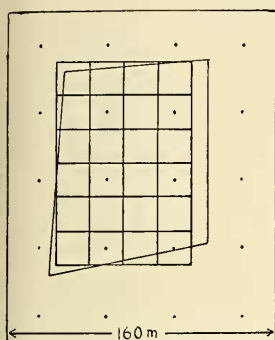
If a plot is provided with a network of catching boxes it is possible to get an idea of the horizontal dispersal of the species from the catches in each box removed every day or every other day during a certain period. Local and temporary differences in the activity induced by diverging climatological circumstances may exercise a disturbing influence. This is most clearly shown by the spider *Lycosa chelata*, which is very active in spots warmed by sunshine and then therefore runs a great chance of falling into a catching box. The differences between the catches in sunny and shady places in the forests are at least partly to be ascribed to a locally and temporarily higher activity of such thermophilous animals. It is clear that these differences only occur with day animals, of which *Lycosa chelata* is the most pronounced. Other local differences may occur in places favourable to night frost, since low temperatures check the activity and night animals run a smaller chance to be caught.

The mutual distance of the catching boxes determines the exactness of our knowledge of the dispersal of a certain species. For species with a great mobility, running long distances (e.g. large Carabidae) a longer distance between the boxes will do than for species with a slight mobility. Boxes at distances of 40 m generally give a fair impression of the dispersal of most species. By moving the boxes over half the distance, it is possible to check whether the result obtained is corroborated in a following period. More detailed results can be had by digging in a number of boxes at distances of 10 or 5 m on a part of the experimental plot of which it is desirable to gain more exact data.

How long the catches must be continued depends on the density and the activity of the species. In most cases two weeks will do to get sufficient data of species that do not occur in too small a density and are not in an inactive stage.

In fig. 13 the results are presented of the most important species. In the first figure the outline of the beech forest investigated is given (compare to fig. 5). The rectangle within it, divided into squares, marks the places of the boxes during the period from 25 IX—11 X 1946 and from 22 IV—3 V 1947: the boxes were dug in in the centres of the squares (mutual distances 20 m). The points in the rectangle around it mark the places of 20 boxes at distances of 40 m during the period from 6 V—13 V 1947, when catches were made over the whole plot including the S.W. and S.E. borders and in strips of the stands bounding in N.W. and N.E. to the beech forest (for description see pp. 50, 51). In the other figures the catching results of each box are given for several species during the period indicated. The values marked with a cross (+) are composed of catchings, of which one had an abnormally high value, increasing the total considerably. The cause of these deviating results is unknown. All other values are based upon rather equable daily catchings. By comparing the diagrams with the first figure localisation in the forest is possible.

The data of *Carabus problematicus* show that this large ground-beetle was caught in greater numbers along the borders than in the centre of the forest. Whether this difference is significant is questionable however. Perhaps this quickly running beetle does not like to penetrate into the bare beech forest. The larva of this species too was caught in smallest numbers in the centre. *Nebria brevicollis* shows a distinct concentration in the S.W. corner of the plot. Increasing the number of boxes in that part showed that the area of high concentration was restricted to a surface of 30×40 m. *Abax parallelus* and *Abax ater* have like *Pterostichus oblongopunctatus* a density distinctly higher in the part of the plot marked III in the description, where the floor has a very loose structure. The available data point to the fact that the dispersal of *Pterostichus* over the plot remained unchanged during the two years of investigation, as was the case with most other species. The catches of 28 VIII—6 IX 1946 fell in a period of low activity of this species, which caused low catches and an indistinct dispersal. *Amara lunicollis* has a considerably higher density under the low vegetation in the stand N.E. from the forest than in the beech forest itself. *Notiophilus* sp. and *Phosphuga atrata* are rather regularly dispersed. *Silpha carinata*, however, shows a distinct concentration in some places situated at the border and N.E. from the forest. *Helops laevis* has a distinct preference for part I of the plot with a compact humus layer. The Staphylinidae are rather irregularly dispersed over the forest. *Agrotis* is supposed to have its largest density in the southern part. Of the Lycosidae, *Trochosa terricola* is abundant throughout the forest. *Lycosa chelata* distinctly prefers the more open vegetation along the N.E.



EXPERIMENTAL PLOT 8G
RECTANGLE AND POINTS INDICATE THE
PLACES OF THE BOXES (SEE TEXT)

7	9	6	12
3	2	3	13
11	2	3	26 ⁺
4	3	2	8
4	7	6	10
12	15	7	13

CARABUS PROBLEMATICUS
25 IX - 11 X 1946

3	-	6 ⁺	1
-	2	-	-
1	1	-	-
1	-	-	1
1	-	1	1
2	1	3	-

CARABUS PROBLEMATICUS
LARVA 22 IV - 3 V 1947

-	2	-	61
-	2	10	23
-	4	2	1
2	1	7	-
2	4	7	1
-	1	4	-

NEBRIA BREVICOLLIS
25 IX - 11 X 1946

-	1	-	1
-	-	1	1
3	-	-	-
1	3	2	-
1	2	9	11
2	1	6	2

ABAX PARALLELUS
25 IX - 11 X 1946

1	1	2	-
-	1	1	-
-	-	2	1
-	6	2	1
1	3	10	6
3	2	2	3

ABAX ATER
25 IX - 11 X 1946

2	-	1	-
2	-	1	1
-	1	-	1
-	-	2	1
10	9	5	2

AMARA LUNICOLLIS
6 V - 13 V 1947

-	-	4	1
-	4	2	4
5	1	-	1
2	3	-	2
5	2	3	2

NOTIOPHILUS SPEC. DIV.
6 V - 13 V 1947

2	2	2	2
1	4	2	3
-	2	2	1
2	3	11 ⁺	7 ⁺
2	5	5	1

PHOSPHUGA ATRATA
6 V - 13 V 1947

Fig. 13. Horizontal dispersal of epedaphic macrofauna species in the beech forest 8 G.

18	-	-	-
2	-	-	1
3	-	-	-
26	2	14 ⁺	1
11	58	2	4

SILPHA CARINATA
6 V - 13 V 1947

10	4	6	6
1	1	3	1
-	-	-	-
-	1	-	-
-	-	1	-

HELOPS LAEVIOCTOSTRIATUS
6 V - 13 V 1947

-	-	1	3
2	5	8	2
-	-	7	1
-	-	-	4
2	-	-	1

OTHUS PUNCTULATUS
6 V - 13 V 1947

5	10	7	1
15	4	11	2
18	14	11	1
3	15	15	4
1	4	13	1

STAPHYLINUS CHALCOCEPHALUS
16 V - 30 V 1947

6	7	10	7
1	13	6	2
3	11	14	13
14	5	5	9
2	16	5	8
5	14	11	8

QUEDIUS LATERALIS
25 IX - 11 X 1946

1	8 ⁺	4	3
1	2	1	1
3	2	1	1
-	-	1	-
1	1	-	-
1	-	1	-

AGROTIS SPEC. LARVA
22 IV - 3 V 1947

10	6	8	5
6	4	11	5
11	16	4	5
7	2	5	3
6	7	9	6
5	8	11	8

TROCHOSA TERRICOLA ♂
22 IV - 3 V 1947

1	3	2	1
1	1	-	3
3	-	2	1
3	1	1	2
6	3	3	4
12	9	15	18

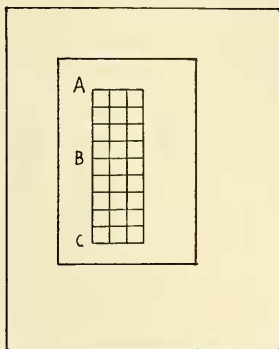
LYCOSA CHELATA
22 IV - 3 V 1947

1	2	1	1
-	1	3	6
3	2	2	-
-	-	-	-
9	-	3	6

JULUS SCANDINAVIUS
6 V - 13 V 1947

Fig. 13 (continued).

-	-	1	2
1	3	2	3
2	1	2	1
-	3	3	4
5	4	5	8

CYLINDROJULUS SILVARUM
6 V - 13 V 1947

PTEROSTICHUS OBLONGOPUNCTATUS 9 V-24 V'46

A	7	7	11
	12	8	11
	20	11	19
B	17	32	26

A	-	-	-
	-	3	2
	2	3	3
	-	4	10
	3	14	10
	5	9	13
	6	1	5
	4	8	2
C	1	7	1

28 VIII-6 IX'46

1	-	2	-
-	2	4	-
5	6	3	2
12	13	8	4
18	19	11	10
7	19	19	6

PTEROSTICHUS OBLONGOPUNCTATUS
25 IX - 11 X 1946

2	2	2	2
1	3	3	4
4	26	19	15
15	22	36	26
16	31	24	18
14	12	17	11

PTEROSTICHUS OBLONGOPUNCTATUS
22 IV - 3 V 1947

7	9	5	6
14	7	20	4
36	54	57	11
15	45	24	25
22	20	27	19

PTEROSTICHUS OBLONGOPUNCTATUS
6 V - 13 V 1947

Fig. 13 (continued).

border. It was already mentioned that contrasts partly may be caused by local differences in activity.

As to the two species of millipedes, the individuals of *Julus scandinavicus* were caught in a much larger quantity in proportion to their density than *Cylindrojulus silvarum*, which agrees with the much greater mobility of the first species. Both occurred spread all over the forest.

2. Day and Night Activity

Direct observations by day already show that the greater part of the epedaphic fauna appears hardly or not at all on the soil surface of the forest. How far the animals are active nevertheless in the litter layer is hardly to say. An investigation into the litter layer cannot inform us about their activity since the animals get alarmed and the activity observed then is no proof of the activity when not alarmed.

The activity on the soil surface at night and by day is to be determined by regularly counting the catches in the boxes at sunset and sunrise.

During three weeks resp. in April, May and June the catches in resp. 24, 20 and 6 boxes were counted in this way. The day observations were made in twilight, the night countings mostly not before some hours after sunrise. For this reason it is possible that the day values are too low and those of the night too high. Some checks done at sunrise exactly and some hours later showed, that during the early morning hours the catches were nil, most likely because of the low temperature in these hours by which activity is checked. It is, however, not probable that this holds universally.

Day and night catches of each of the three weeks were joined and inform us about the activity of the species by day and by night. Because of the difference in length between night and day the proportion between the two numbers is not the proportion between day and night activity. Moreover, both are so much influenced by changing weather conditions that a calculation of this relation has no sense in my opinion. Only when there is a constant and great

Table 22. Ratio of day and night catches in April, May and June 1947.

Catching period	24IV-30IV	6 V-13 V	27VI-3VII	2VII-5VII	Total
Day/Night ratio in hours	15 : 9	51 $\frac{1}{2}$: 8 $\frac{1}{2}$	19 : 5	19 : 5	
<i>Carabus violaceus</i> . . .			0 : 7	0 : 5	0 : 12
<i>Carabus violaceus</i> larva .	9 : 6	5 : 0			14 : 6
<i>Carabus problematicus</i> . .		0 : 4	0 : 3	0 : 4	0 : 11
<i>Abax parallelus</i>		8 : 31	2 : 12	0 : 4	10 : 47
<i>Abax ater</i>		0 : 16	0 : 1	0 : 7	0 : 24
<i>Pterostichus oblongopunctatus</i> , ♀	59 : 67	75 : 65			
<i>Pterostichus oblongopunctatus</i> , ♂	20 : 74	56 : 74			
<i>Pterostichus oblongopunctatus</i> , ♀ + ♂ . .	79 : 141	131 : 139	3 : 7	0 : 3	213 : 290
<i>Pterostichus niger</i> . . .				0 : 2	0 : 2
<i>Pseudophonus pubescens</i> .			0 : 7		0 : 7
<i>Notiophilus</i> sp. div. . .	12 : 8	10 : 20			22 : 28
<i>Amara lunicollis</i>		13 : 14	4 : 1		17 : 15
<i>Staphylinus chalcoccephalus</i>		23 : 9		31 : 11	54 : 20
<i>Othius punctulatus</i> . . .	6 : 6	6 : 18			12 : 24
<i>Philonthus decorus</i> . . .	15 : 3	7 : 8			22 : 11
<i>Phosphuga atrata</i>	1 : 12	12 : 27			13 : 39
<i>Silpha carinata</i>		26 : 66	2 : 7		28 : 73
<i>Geotrupes silvaticus</i> . .			11 : 0	2 : 0	13 : 0
<i>Helops laevioctostriatus</i> .	2 : 23	0 : 18			2 : 41
<i>Byrrhus pilula</i>			0 : 6		0 : 6
<i>Julus scandinavicus</i> . . .	0 : 12	3 : 13			3 : 25
<i>Cylindrojulus silvarum</i> . .	1 : 9	1 : 10		0 : 1	2 : 20
<i>Agrotis</i> sp. larva	0 : 18				0 : 18
<i>Trochosa terricola</i> . . .	55 : 115				55 : 115
<i>Lycosa chelata</i>	87 : 7				87 : 7

difference between day and night catches it may be concluded that a species is a day or night animal.

In table 22 the collective day and night catches of the three weeks have been given. It is clear that the larger Carabidae, *Carabus violaceus*, *C. problematicus* and *Abax ater* are exclusively active at night. The number of catches of *Pterostichus niger*, *Pseudophonus pubescens*, *Agrotis* larvae and *Byrrhus pilula* is too small to draw the same conclusion from this material. Further, the following species were mainly caught at night and may be so mainly active at night: *Abax parallelus*, *Phosphuga atrata*, *Silpha carinata*, *Helops laevioctostriatus*, both millipedes *Julus scandinavius* and *Cylindrojulus silvarum* and *Trochosa terricola*. The smaller Carabidae, *Pterostichus oblongopunctatus*, *Notiophilus* sp., *Amara lunicollis* and the larvae of *Carabus problematicus* were caught both by day and by night. This was also the case with the Staphylinidae, *Staphylinus chalconecephalus*, *Othius punctulatus* and *Philonthus decorus*. Of the species caught in sufficiently large numbers only *Pterostichus oblongopunctatus* shows a distinct difference between day and night activity in April and May. The small day catches in April are chiefly to be attributed to the low day catches of the males in this period. This points to a low day activity of the males during that period, the cause of which is unknown. *Geotrupes silvaticus* and *Lycosa chelata* were caught exclusively or almost exclusively by day.

3. Catching Fluctuations during the Course of the Year

Both activity and population density of the epedaphic fauna change in the course of the year.

In the first place activity is influenced by climatic factors, of which temperature and moisture have the most distinct influence. In the low autumn temperatures a great part of the fauna becomes inactive or the activity decreases strongly. This is continued during the winter, but with increasing temperatures in spring the activity increases again. Concerning the influence of moisture it is mainly a long continued drought in summer which dries up the floor considerably and so diminishes the activity of the fauna. Some showers of rain can abruptly end this period of inactivity.

Next to these external factors there are also internal factors causing seasonal changes in activity: reproduction may stimulate activity, an inborn cyclical factor expressing itself in aestivation and hibernation may lower activity and even bring it to a standstill: diapause. Supervention of this phenomenon may also be influenced by environmental conditions.

The population density of the epedaphic macrofauna is also liable to change. If we confine ourselves to species with a complete metamorphosis (e.g. Coleoptera) it is of importance to consider separately larvae and adults, since both groups have marked differences in life habits, mobility etc. The appearance of the imagines especially when this takes place in a brief span of time, will greatly

increase the density of the adults or even bring it from nil to a certain value for species with an adult life term less than a year (Siphidae). Dependent on the length of the oviposition period the larvae appear suddenly in great numbers or during the course of a longer span of time. Generally the youngest stages are not caught by means of the catching boxes and the older stages in a less degree than adults.

Decrease of the population density takes place gradually because of an attack of predators, parasites and diseases or suddenly because of pupation (in the case of larvae), reaching the age limit, especially if the term of life is short, or because of epidemics.

Lastly changes in the population density can also be caused by immigration into or emigration from the experimental field.

Both fluctuations in activity and changes in the population density find their expression in the catches of the boxes if they are executed on the same plot during a full year and the animals caught are released again.

The catches made in 1946 and 1947 were executed in different forests and to a varying extent. Still from the results it is possible to get a rough impression about the fluctuations in activity and population density in the course of a year.

To get a survey of the course of the catches of the different species, graphs were made of the results during two succeeding years (March 1946—October 1947). Interruptions longer than one week were made in June 1946 and July 1947 (resp. 5 and 3 weeks) and in winter from October 1946 to the end of March 1947. During the latter interruption some boxes were left in the soil in autumn and the contents were controlled several times. As was to be expected the activity in winter was very small and limited to some species only: the larvae of *Carabus problematicus*, millipedes and the larvae of *Cantharis*.

Both in 1946 and in 1947 most catches were made in the beech forest 8 G. The animals caught were released on the same plot, though in some cases only after the lapse of some time. In 1946 the catches were also made in the adjoining plots 8 K (beech) and 8 H (oak), already mentioned in the description of the environment (for situation see fig. 4). In 1947 catches were made in these forests but then also in a neighbouring beech forest 9 F of the same age as 8 G, in two young oak forests 9 D and 7 B (both comparable to plot 8 H) and in a pine forest 9 A, the epedaphic fauna of which did not differ much from that of the adjoining hardwood forests, mentioned above.

In fig. 14 the results of the two years are given. The forests concerned are marked at the top of the diagram, the number in parentheses behind them indicates the number of boxes used in catching. The columns which give the number of individuals per box per week are made black as far as they concern catches in plot 8 G. These data are the best for mutual comparison. The other columns concerning catches in the other forests are cross-hatched.

FLUCTUATIONS IN CATCHES OF EPEDAPHIC MACROFAUNA

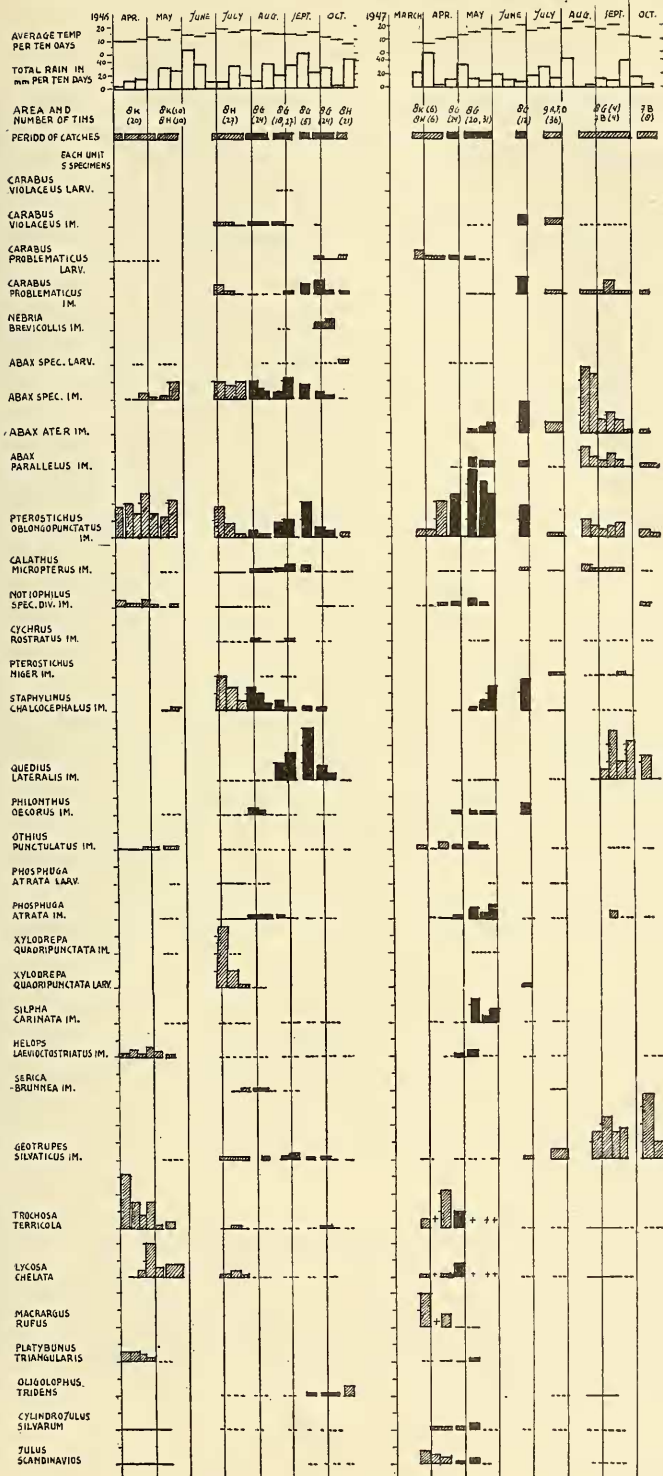


Fig. 14. Catching results in several adjoining forests during the years 1946 and 1947.

If the average remained below 1 it was indicated by a horizontal black line, if only some individuals were caught it was marked by a broken horizontal line.

The fluctuations in catching will be discussed for each species separately in the special part, together with the phenological data. In general we see that each species has a specific period in which it is caught most numerous.

Spring was characterized by large catches of *Pterostichus oblongopunctatus*, *Trochosa terricola* and *Lycosa chelata* and (in 1947) of *Macrargus rufus*. Rather large numbers were caught of *Helops laevioctostriatus* (nearly all males, see p. 37), *Notiophilus spec.*, *Othius punctulatus*, *Platybunus triangularis* and the millipedes *Cylindroiulus silvarum* and *Julus scandinavicus*.

In the early summer (May-June) the Carabidae *Pterostichus oblongopunctatus*, *Abax ater* and *parallelus* and *Carabus problematicus* were numerous, as well as *Staphylinus chalconcephalus* and the Silphidae *Phosphuga atrata*, *Xylodrepa quadripunctata* and *Silpha carinata*.

In summer (July-August) a decrease of the catches especially those of *Carabus problematicus* and *Pterostichus oblongopunctatus* was observed. *Carabus violaceus*, however, was caught most during this time. In 1946 catches of the larvae of *Xylodrepa quadripunctata* were most abundant.

In autumn, finally, *Quedius lateralis* and *Geotrupes silvaticus* stood out. Of the Carabidae *Carabus problematicus*, *Nebria brevicollis* and *Pterostichus oblongopunctatus* were numerous. Also the harvester *Oligolophus tridens* was numerous caught.

It is clear that these different seasonal aspects of the epedaphic fauna, living predatorily for the greater part, are of great importance to the community of the forest soil. With a greater density and activity a species will take a heavier toll of its fellow-inhabitants. On the other hand these factors will also influence the kind and the degree of the attack, the species itself undergoes from its predators.

Concerning the factors influencing activity and population density it is not possible to draw any conclusion from changes in the catches since all these factors cooperate in the catching results.

By means of climatic observations on the one side and examination of the animals on the other — in order to determine sex, development of the gonads and, if possible, the age of the animal — it is possible to interpret the fluctuations in outline.

b Special Part

The discussion below of the different species is based upon catches of 1946 and 1947. The differences observed in the two years for some species point to a variation in the period of activity and in the time of sexual maturity as dependent on climatic factors. Since the catches of 1947 were checked more in detail than those of 1946 we take the former as the starting point and compare them with those of 1946.

Only in the case of Carabidae the gonads were examined on different times of the year to gain some insight in reproduction of these species. For Silphidae and *Geotrupes* the detailed informations of HEYMONS et al. and v. Lengerken are sufficient in this respect.

Concerning nomenclature MROZEK DAHL (1928) is followed for Carabidae, REITTER (1908-'16) for other Coleoptera species and ROEWER (1929) for Aranea.

For all discussions reference must be made to fig. 13 (horizontal dispersal) fig. 14 (seasonal fluctuations) and table 22 (day and night activity).

In the estimations of the population densities the values are expressed in numbers per a (are = 100 m²).

Carabidae

Carabus violaceus L.

In 1947 in the 2nd and 3rd week of May the first imagines were caught in small numbers. They were exclusively females, the gonads of which were hardly developed. In the last week of May males were also caught. All animals possessed well-hardened elytra: they hibernated as adults once or twice already. During the month of June the youngest generation which hibernated as pupa appeared, still with weak elytra. Their ratio to the old generations was about 2 : 1. The predomination of the young animals in the catches is supposed to prove a real difference in density of these two groups since no difference in activity could be stated. Gradually the elytra of the young animals became hard, so that at the end of July only few animals with weak elytra were caught. During July and August the eggs were deposited. In this period the sex ratio of the animals caught was about 1 : 1. Afterwards the catches decreased strongly, though a single animal (always with hard elytra) was still caught as late as October. In the latter part of the summer of 1947 hardly any larvae of this species were caught, whereas they were often caught in 1946 during the same time. The very dry weather is presumed to have been unfavourable to the activity of the larvae. Carabidae larvae are known to be very susceptible to drought (KERN 1921).

Carabus violaceus was found in all forests investigated; even in coniferous stands without any undergrowth it occurs rather numerously. It had its greatest density in the pine stand 9 A with an abundant undergrowth of shrubs. The dispersal of the species in the different forests examined appeared to be rather regular: as was to be expected for this great and very mobile species, aggregations did not occur.

Like the other large Carabidae it is nocturnal in its habits, preying on the soil surface, and by day only leaving its hiding place when it is disturbed.

The digestion of the food takes place externally, so no conclusions concerning the food can be drawn from the contents of the stomach, consisting in this case of a dark brown fluid. That it is not particular in choosing its prey appeared from the fact that

it ate even larvae of the pine sawfly *Diprion pini* L., which are despised by many predators because of the high content of resin. As a predator of pupating caterpillars it must be of importance for the balance of the whole forest community, though direct investigations in this field are not known to me.

The density of this species could not be established because of the sparse population; it may be valued at 1 - 3 per a in the beech forest 8 G.

Carabus problematicus Herbst

The imagines of this species did not become active before May either. The animals caught then hibernated as adults. Like with *Carabus violaceus*, in the beginning the females dominated strongly in number (6 V - 30 V: 21 females to 3 males). At the end of June the young imagines appeared, which like those of *C. violaceus* dominated the old ones (24 VI - 1 VII: 25 young to 6 old). During July and August the species was caught in low numbers, a phenomenon which was observed both in 1946 and 1947 and which is mentioned for several Carabidae in literature (DELKESKAMP 1930: *C. nemoralis*, *Procustes coriaceus*; GERSDORF 1937). Development of the gonads and mating did not take place before the end of August, when the animals waked from their "aestivation" and were again caught in large numbers. The elytra of the young animals were quite hard now and also in this species the sex ratio was almost 1 : 1. Up to October eggs were deposited, the larvae were frequently caught throughout the winter till the middle of May.

In contrast to the imago, which is a distinct nocturnal animal, the larvae is active both by night and by day.

As to digestion *C. problematicus* behaves like the preceding species. In consequence of their fairly insimultaneous activity in the course of the year the two species will not compete with each other.

Some preference for one of the forests investigated could not be discovered. On the border of the beech forest 8 G the catches were larger, which may point to an aversion to forests without any undergrowth.

The density is somewhat higher than that of *Carabus violaceus* and is valued at about 5 per a.

Carabus nemoralis Müll.

This species occurs only little in the stands investigated. In both years imagines were caught from the beginning of March to the end of May.

DELKESKAMP (1930), who made a detailed study of *Carabus nemoralis* stated this species to reproduce in spring, to "aestivate" from the end of May to the middle of July and to be still active to some extent afterwards. The young imagines were stated to appear from July and sometimes already mated in autumn.

In this investigation the species was only caught in the period

of greatest activity (reproduction period), which is comprehensible because of its small density.

As was already said, fixing the density of the *Carabus* species mentioned by means of the Lincoln-index was impossible. The following case will show this. In a formation of 50 catching boxes, at mutual distances of 20 m taking together a surface of about 120×120 m, more than a hundred marked animals were released in the centre. During the succeeding fortnight only some individuals were recaptured on the first three days, partly in boxes far away, so that it may be concluded from this that obviously the greater part of the animals left the experimental plot already within some days.

Abax ater Vill.

The imagines of this species became active in the beginning of May. The sex ratio of the individuals caught does not point to an earlier or larger activity of the females, as in the case of the *Carabus* species, rather the opposite (6 V - 23 V 1947: 30 males to 53 females). In these catches both young and old imagines occurred. Already a fortnight after appearance ripe eggs were found in the ovaria of some old females, so that it may be supposed that these were females which did not come to oviposition in the preceding year. In the young females eggs developed and were deposited in the course of summer and autumn. Probably in consequence of the dry summer in 1947 no eggs seemed to be developed in the ovaria in the autumn of that year, but in 1946 eggs were certainly deposited in that season since larvae with lengths of 2-5 mm were found in the samples of October and November, and up to May large larvae were caught which were no doubt deposited as eggs in autumn. Whereas in 1946 larvae were caught throughout the year, in 1947 they were only caught before summer, probably for the same reason. From these facts it is supposed that in contrast to the *Carabus* species, *Abax ater* reproduces in spring (old females), summer (old and young females) and autumn (young females). In accordance with this supposition both young and old beetles were caught in spring, summer and autumn. Towards winter the number of animals with weak elytra decreased strongly, so no hatching of imagines took place then.

The sex ratio of animals caught in the period from the middle of May to the middle of September (420 f : 382 m) deviated a little more from equal numbers than for most other species. Before this period the males dominated, after it the females.

Day and night catches showed that this species has nocturnal habits.

In examining the contents of the stomach many parts of chitin were often found, mostly remnants of Collembola and other small arthropods. Sometimes the stomach was filled with blood when the animal had fed on the dead body of some mammal or bird. In other cases mould hyphae and algae were found, vegetable rests of food were exceptions, however.

Abax ater is more abundant than the other *Abax* spec. in the area concerned. It is found in all forests investigated, though in different densities. The highest densities occur in places with a rather loose structure of the floor. Like many Carabidae it avoids dry forests: on a dry southern slope, grown with young oaks, the density was three times smaller than on the corresponding moist northern slope.

In the central part of the beech forest 8 G the population density calculated for this and the next species together was 120 per a. In 1947 the numbers of individuals caught of *Abax ater* and *A. parallelus* were resp. 477 and 265 in this forest. It seems probable that *A. ater* as a nocturnal animal has a smaller chance to be caught than *A. parallelus*, which is also active by day. So its density may be estimated to be about twice as large as that of *parallelus* and thus amounts to about 80 per a on the experimental plot.

Abax parallelus (Duftsch.)

The phenology of this species differs much from that of the preceding species. The catches beginning at the end of April wholly existed of old specimens both males and females. Eggs did not develop in the ovaria before the middle of May. Matings were often observed. The eggs were deposited in June, afterwards the catches of imagines decreased. In August they increased again strongly, then the greater part (80%) existed of young animals. After some weeks the elytra of these animals were hardened, so that young and old imagines were externally indistinguishable. Sexual maturity was not reached until the next spring.

The contents of the stomach agree with that of *Abax ater*. Still this species will take another place in the community because of its smaller size and its activity also by day. It is less generally dispersed in the area examined than *A. ater*, while its density is also smaller in the biotopes in which both occur. In the central part of the beech forest 8 G it was about 40 per a. Like the preceding species *A. parallelus* seems to prefer a rather loose structure of the floor.

Pterostichus oblongopunctatus (Fabr.)

The imagines of this species were caught from the end of March. In the first weeks males strongly dominated. Afterwards almost equal numbers of the two sexes were caught (from the middle of April to the end of May 918 f : 857 m). Mating was often observed from the beginning of April to the end of May. The development of the ovaria took place in April, the eggs were laid from the end of April to June. Afterwards a period of slight catches of imagines followed during July and the first part of August in consequence of the inactivity of the animals. During this period the number of females caught was higher than that of males. From the middle of August the catches increased again, then the sex ratio was almost 1 : 1. A great part of the animals caught now was young. It was impossible to state this ratio with certainty as the

old animals have also rather weak elytra. Though the density of this species on the experimental plot was certainly larger in the spring of 1947 than in the spring of 1946 the increase of the catches in autumn was much smaller in 1947 than in 1946. The unfavourable influence of the extreme drought in 1947 will have been very probably the cause of it.

Of the forests examined, deciduous stands were populated most densely. The largest density was here again found in places where the floor had a loose structure. According to a census in May 1947 in the forest 8 G the density was about 250 per a (see table 10 and text p. 47).

In this species the contents of the stomach also mostly consist of rests of the cuticles of small insects, chiefly Collembola. Vegetable rests were not found. No more than in other species this means, however, that this species may not feed on vegetable material in other biotopes with an undergrowth of herbs. FORBES (1880, 1882) already determined by means of examination of the stomach of a large number of Carabidae of different biotopes that the greater part of the species feeds both on animal food and such vegetable food as grasses and seeds. In the forest 8 G without undergrowth, however, the food appeared exclusively to consist of animal material.

Pterostichus niger (Schall.)

This species was caught in rather small numbers of imagines only, and not before July. Then the animals caught were young ones for the greater part. At the end of July a number of females had eggs which were probably laid in August. The catches in September yielded exclusively old imagines. The catching results were too small to say anything with certainty about the phenology of this species. The stomach of this species too contained chitin remnants of animal preys.

Of the other Carabidae only the numbers of *Nebria brevicollis*, *Calathus micropterus*, *Notiophilus* sp. and *Cychrus rostratus* are graphed.

Nebria brevicollis (Fabr.) was caught in large numbers in a small part of the forest 8 G during the autumn of 1946 only (see for the dispersal fig. 13). The next spring the young larvae of this species were caught in the same place. Later on in the year neither the larvae nor the imagines were caught, however, so that it is probable that the species has not maintained itself there (perhaps in consequence of the dry summer?).

Calathus micropterus Duftsch. was caught in small numbers throughout the year, but most numerous in autumn. The catching method is unsuitable for this small species (see p. 36), so that the results give no correct impression of its density. Considering the catches in 4 dm³ samples, in which it occurred regularly, the density must be valued at some hundreds per a in the forest 8 G.

Of *Notiophilus* several species were caught. Most numerous

was *N. biguttatus* (Fabr.) and *N. rufipes* Curt. A third species *N. palustris* Duftsch. was caught less. As to the catching method, the same holds good for these species as for *Calathus micropterus*. Their joint density is also certainly some hundreds per a.

Cychrus rostratus (L.) was caught throughout the year though only in small numbers because of its small density. Its density in the beech forest is valued at some specimens per a. Being a mollusc-eater its most important prey is no doubt *Arion subfuscus* here. It was indeed often observed attacking this slug.

Of the Carabidae, only caught rarely in the beech forest 8 G, ought to be mentioned: *Calathus fuscipes* (Goeze), *Poecilus lepidus* (Leske), *Poecilus coerulescens* (L.) and *Amara lunicollis* Schiødte, which were mainly found in open areas and along the sides of the road and probably penetrated from there into the forest, *Pterostichus strenuus* (Panz.), *Platynus obscurus* (Herbst), *Stomis pumicatis* (Panz.), *Leistus rufomarginatus* (Duftsch.), *Loricera pilicornis* (Fabr.) and *Harpalus latus* (L.), which are real inhabitants of the forest: they occurred only in small density in the forest examined. Finally *Calosoma inquisitor* L. is to be mentioned, which was caught in a small quantity only in spring. The imagines of this species chiefly inhabit the tops of trees where it is living on caterpillars.

Staphylinidae

Staphylinus chalconecephalus F.

This most numerous species of the Staphylinidae was caught in the catching boxes from May to October. The largest numbers were caught between the end of June and the end of August, the period of the largest activity of this species. Probably in consequence of the extreme drought in the summer of 1947 this species was only caught in small numbers then. From the results in the forest 8 G it appears that *S. chalconecephalus* has its largest density in the centre of the forest: about 50 per a according to a census in July 1946. The food of this species consists of soil animals and carrion. It was seen feeding on collembolids, spiders and harvesters. The contents of the stomach consisted of a dark-brown fluid, and so did not give any indication about the identity of the prey. The species is attracted by the smell of carrion, as is shown by the large numbers caught in a box with the dead body of a mouse. VORIS (1934) considers predation the dominating habit of feeding in Staphylinidae. The animals are active both by night and by day.

Quedius lateralis Gray

This staphylinid, somewhat smaller than the preceding species was caught only in small numbers during spring and summer. From the end of August to the middle of October it was, however, caught in very large numbers. So it replaced the preceding species in the catches, which was rarely caught then. In consequence of the drought in 1947 it was not caught before September that year. It was rather regularly dispersed in the beech forest 8 G and its

density is valued to be a little higher than that of *Staphylinus chalocephalus*. Like this species it is also attracted by carrion.

Of the other Staphylinidae *Philonthus decorus* Grav. and *Staphylinus brunnipes* F. were only caught in small numbers because of their small density. *Othius punctulatus* Goeze and *Othius myrmecophilus* Kiesw. were also caught in small numbers but this was caused by the fact that the method did not suit these small species.

Rarely caught were : *Staphylinus olens* Müll., *Staphylinus stercorearius* Oliv., *Quedius fuliginosus* Grav. and some other *Quedius* species.

Silphidae

Phosphuga atrata L.

The imagines of this species were regularly caught in the boxes from April onwards. According to HEYMONS et al. (1927), who made a detailed study of this species, the animals lay their eggs separately in the soil from the middle of April to the end of August. One female is able to deposit as many as 160 eggs totally. After reproduction the old animals die. The young imagines develop in about 50 days from the eggs and then burrow into the soil. Both imagines and larvae prefer slugs and snails as prey.

In the spring of 1947 the catches were higher than in 1946. This is supposed to be attributable to the favourable feeding circumstances for the larvae in 1946 when there were many young *Arion subfuscus*, especially in the early spring. In the dry summer of 1947 the catches were very small. The density in the forest examined, in 1946, may be valued at some tens per a.

Xylodrepa quadripunctata L.

Also to this species HEYMONS et al. (1928) devoted an extensive study, from which I derive the following facts. The imagines feed on caterpillars and other insect larvae in trees. Oviposition takes place in May. During 2-3 weeks on an average every day one egg is deposited in the soil. The larvae develop in about 7 days from the eggs. They live on the soil surface and chiefly feed on insects just dead but they take also living preys. After a development of about 50 days — of which about 30 as pronympha and pupa — the young beetle hatches but remains hidden in the cavity of the pupa till the next year. After reproduction the adults remain some time active in trees but from the middle of July they enter into the soil and die.

The catches tallied with these statements. The imagines were caught only from spring to the middle of July, the larvae were caught in May and June. In the beech forest 8 G the species only occurred along the N.E. border, with many young oaks. In the adjoining oak forest 8 H the density was much greater and especially in June 1946 the larvae were caught there in large numbers.

Silpha carinata Hrbst.

According to HEYMONS et al. (1932) the cycle of life agrees most with that of *Phosphuga atrata*. The larvae and imagines prey on living animals.

The species was caught in the boxes throughout the year. In May 1947 it appeared to be strikingly heterogeneously dispersed: fig. 13. Causes and significance are unknown.

Of the other large Silphidae the following species ought to be mentioned: *Oceoptoma thoracica* L., *Necrophorus vespilloides* Hrbst., *Necrophorus vespillo* L. and *Necrophorus humator* F., all of them species which were only caught in the boxes with carrion as a bait. This was also the case with the two Histeridae *Hister cadaverinus* Hofm. and *Hister striola* Sahlb. Usually none of these species was caught in large numbers, though they were attracted by a bait. The population density must be of quite another order of size as that of the species discussed above and may possibly be expressed in rather small numbers per ha.

Scarabaeidae

Geotrupes silvaticus Panz.

This species is by far the most numerous dor beetle in the forest. According to v. Lengerken (1939) in May and June the females lay their eggs in pills, which may be composed of excrements of mammals, pine needles, toadstools, pieces of bark or even newspaper. These pills are about 12 cm long and are put 35-60 cm beneath soil surface. The larva spends as much as a year in the soil, in which time the pill is half eaten. Then it pupates and appears as a young beetle after 3-4 weeks. Sexual maturity is not reached before the next year.

During the whole year *Geotrupes silvaticus* was caught in the boxes. Especially in the latter part of the summer in 1947 many animals were caught. The greater part of them were young animals, recognizable by the weak elytra. Both by night and by day the animals are active. In view of their great mobility it is impossible to determine their density by means of the recovery method. The animals are strongly attracted by carrion. Several times hundreds of individuals were caught in a box in 24 hours in this way. A reliable estimation of their density is not possible in the present state of affairs.

Serica brunnea L.

This species was regularly caught in the months of July and August, but only in small numbers. This points to a low density as the mobility of this species is rather great. It seems to prefer deciduous forests: it was always caught here in a greater number than in coniferous forests.

Of the other Scarabaeidae the following species were rarely caught: *Geotrupes vernalis* L., *Geotrupes spiniger* Mrsh., *Ceratophyus typhaeus* L. and *Trox sabulosus* L., all of them species which are not true inhabitants of the forest, but are to be considered accidental guests.

Tenebrionidae

Helops laevioctostriatus Goeze, living on dead wood and other plant materials was only caught in the reproduction period April—May. In the beech forest the species was by far the most numerous in the S.W. part. Here also the larvae occurred in the greatest density (see p. 115). The density of the imagines was not ascertained but may be valued at about hundred per a there.

Of the other beetles, that were caught in the boxes, the imagines of the geophiles must be mentioned, which spend only a short part of their life on the soil surface, mostly immediately after hatching and in the oviposition period. The following species were caught in small numbers: *Athous subfuscus* Müll., *Agriotes aterrimus* L. (both Elateridae) and *Systemocerus caraboides* L. (Lucanidae). In some respect *Calosoma inquisitor* L. (Carabidae) and *Xylodrepa quadripunctata* L. (Silphidae) mentioned above also belong to them. In spite of the rather great density of larvae of Cantharidae not any specimen of the adults was caught in the boxes.

Large Soil Spiders

Next to the soil beetles the larger soil spiders often constitute a large part of the catches in the boxes. Especially in spring and in early summer, during the period of reproduction, when the animals are very active, large numbers were caught. In the beech forest 8 G the two Lycosidae *Trochosa terricola* Thor. and *Lycosa chelata* (Müll.) occurred in great density.

Trochosa terricola Thor. appeared both years somewhat earlier than the other species. It was chiefly caught at night, and appeared rather regularly dispersed over the plot. In March and April there were only some females among the animals caught. Later on, in May and June, the males became rare and the catches, which were very low then, consisted predominantly of females, at first bearing a cocoon with eggs, later on a parcel with young spiders. After the month of July the catches were still lower and then partly consisted of young animals. The density in the forest 8 G was valued at some hundreds per a.

Lycosa chelata (Müll.) is active by day exclusively. It was especially caught in the borders and in the lighter parts of the beech forest. For this species too the catches in spring consisted for the greater part of males, in June the number decreased and the animals caught then were chiefly females, bearing a large egg cocoon on the abdomen. The density of *Lycosa chelata* is very high in the open borders of the beech forest investigated: it may be valued at 700—1000 per a.

Of some importance were also the species *Macrargus rufus* Wid. (Linyphiidae) and *Agroeca brunnea* (Blackw.), both of which were chiefly caught in spring.

The other species of spiders and harvesters were already mentioned above in dealing with the hemiedaphic macrofauna. The most numerous of the harvesters were the species *Platybunus triangula-*

ris (Herbst), which was caught in spring only and *Oligolophus tridens* (Koch), which was chiefly caught in autumn.

E. GENERAL SURVEY OF THE ANIMAL COMMUNITY IN THE FLOOR

The results given in the preceding sections are far from sufficient to obtain a complete insight in the structure and the food chains in the animal community in the floor. For this the data on several groups (nematodes, Diptera larvae, collembolae) are insufficient, on other groups the data fail at all: microfauna, megafauna. Moreover much more details — both in qualitative and in quantitative respect — have to be known on the feeding habits of the numerically important species. However, it may be attempted here to survey in quantitative respect the groups of animals discussed in the preceding parts.

On what basis the densities of these groups have to be compared?

STÖCKLI (1946) called attention to the fact that most organisms inhabiting the soil only live in part of the substrate. Only the "endogae" fauna (geophagous and digging organisms) is able to use the whole substrate. The "cavernicole" fauna (the inhabitants of the cavities in the soil), to which belongs the greater part of the soil fauna, is limited to the pores and cavities in the soil exceeding them in size. An exact knowledge of the volume and the diameter of the pores in the soil would be necessary to establish which part of the substrate is available for a certain species as living space. To this abode, and not to the whole substrate the population density should refer. Though in principle this train of thought is correct, it should be remembered that the total volume of pores and cavities exceeding the size of a certain species is not always available for that species. If the sizes of the cavities are very large in proportion to the sizes of the animals, they will live on the walls of these cavities and the total surface of the walls will be an exacter basis for the density than the volume of the cavities. This circumstance applies to the layer of litter: the space between the solid elements exceeds the sizes of the animals by far, at least those of the micro- and mesofauna. So these groups must be considered inhabitants of the surface of the litter parts. FORD (1938), who examined the density of the microarthropods of a Bromus vegetation, calculated a rough value for the surface of the leaves between which the animals live. In principle this is also possible in the uppermost litter layer. In the deeper layers, however, where the parts of litter are already more or less attacked, this becomes very difficult, while it is quite impossible in the humus layer. So it is not practicable to express the animal density in all layers per unit of surface and consequently the surface unit is unsuitable as a basis for comparing the densities in the different layers. Moreover a comparison on this basis would not be possible for animals of different groups of size e.g. meso- and macrofauna, since the latter, in contrast to the former, does not live on the litter particles in consequence of their large size.

In the organic forest floor there is no severe objection to take the volume of the samples as a basic unit for the population density of the meso- and macro-litter fauna. The technique of sampling prevents large cavities remaining in the samples, so that the contents are to be considered approximately the living space of the mesofauna too.

In order to visualize the average composition of the animal community in the forest floor investigated a diagram was composed (fig. 15).

The average densities of the microarthropods refer to the period from May 1944 to March 1946 (table 13), those of the macroarthropods to the year 1946 (table 16). Of the seasonal geophiles, inserted in the diagram, the average densities refer to the period of occurrence (table 16). The densities of nematodes, rotifers and tardigrads are incidental figures: samples of 21 II 1947 (table 15). The densities of the most important species of the epedaphic macrofauna refer to estimations (partly based on calculations) in the summer of 1946 and are collected in table 23.

Table 23. Population density and population volume of the epedaphic macrofauna.

	Density per a	Density per 40 dm ³	Individual volume in mm ³ (measured)	Individual volume in mm ³ (calculated)	Volume per 40 dm ³ in mm ³
<i>Carabus violaceus</i> . . .	2	0.02	700	700	14
<i>Carabus problematicus</i> . . .	5	0.05	650	700	33
<i>Abax ater</i>	60	0.6	350	312	210
<i>Abax parallelus</i>	30	0.3	200	240	60
<i>Pterostichus oblongopunctatus</i>	180	1.8	100	100	180
<i>Notiophilus</i> sp. div. . . .	200	2		8	16
<i>Calathus micropterus</i> . . .	100	1		30	30
<i>Staphylinus chalicephalus</i>	40	0.4	150	140	60
<i>Quedius lateralis</i>	60	0.6	50	40	30
<i>Posphuga atrata</i>	30	0.3	60	60	18
<i>Trochosa terricola</i>	400	4	70	80	280

The densities of mesofauna and hemiedaphic macrofauna refer to an abode of 40 cm³ for the former and of 40 dm³ for the latter group. To be able to express the densities of the epedaphic macrofauna in the same volume, the values for the density per a were calculated with reference to densities per 40 dm³ of the A₀ layer in total. For this calculation the factors deduced in table 17 were used.

A surface of 100 m² of the forest floor (with an average thickness of the different layers) contains $100 \times \frac{8}{5} \times 4$ dm³ of the F₀ layer + $100 \times \frac{8}{3} \times 4$ dm³ of the F layer + $100 \times \frac{11}{2} \times 4$ dm³ of the H layer = $100 \times \left(\frac{8}{5} + \frac{8}{3} + \frac{11}{2} \right) \times 4$ dm³ = $\pm 100 \times 40$ dm³ of the A₀ layer in total. This value agrees with an average

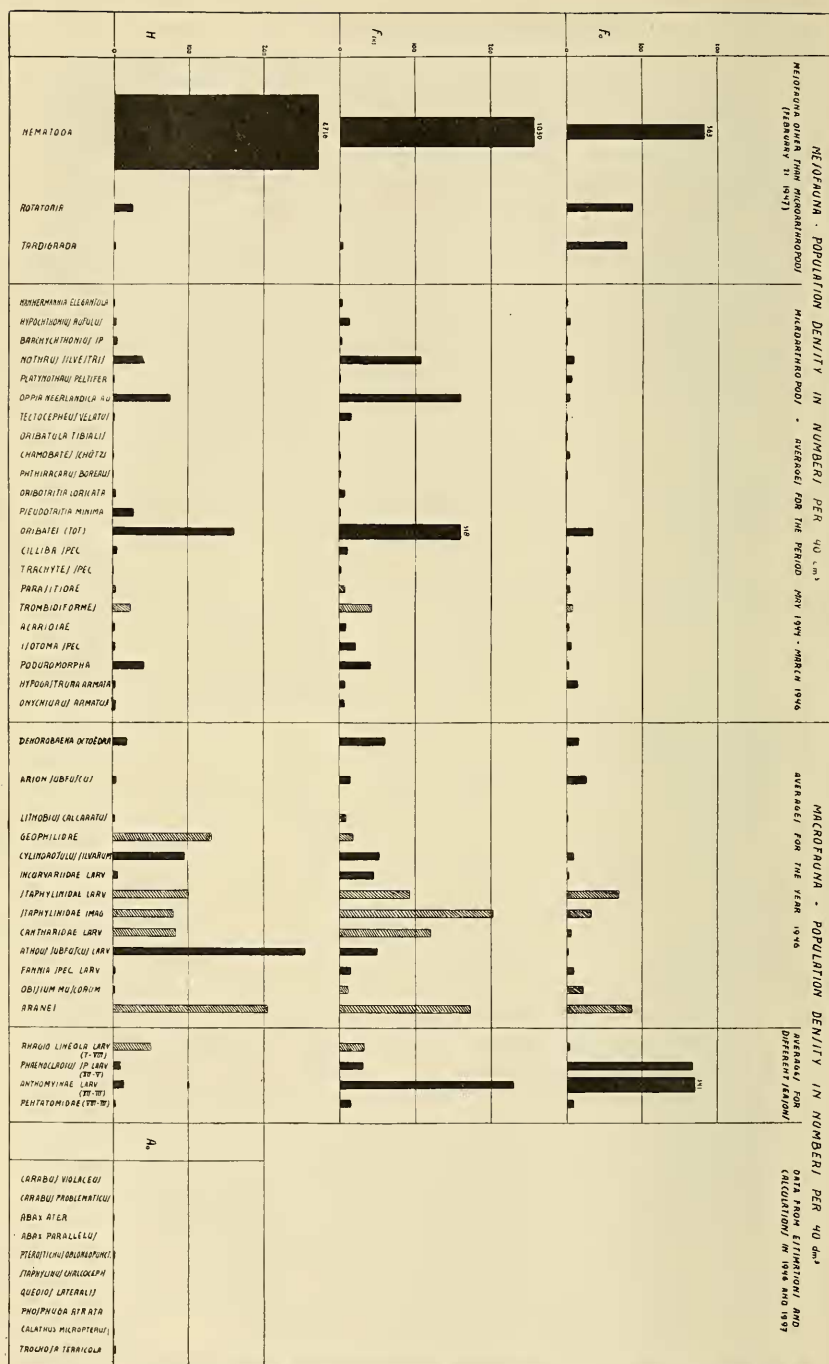


Fig. 15. The average composition of the animal community in the floor of the beech forest 8 G, expressed in terms of population density.

depth of 4 cm for the A_0 layer in compact state. Supposing that the vital functions of epedaphic beetles and spiders, during the period of activity, take place in the A_0 layer their population density per 40 dm³ A_0 is one hundredth of their density per a (= 100 m²). These values contain inaccuracies of 20—40 % (see p. 101).

As was mentioned above the densities of the meso- and macrofauna refer to different periods of observation. The results of the investigation into the quantitative composition of the microarthropod fauna in the years 1945 and 1946 make it unlikely, that the densities in 1945 differ in a high degree from those in 1946. Hence it is permissible to compare the densities of the microarthropods with those of the macrofauna to get a rough insight into the proportion of the numbers. The data of the nematodes, tardigrads and rotifers are incidental and must be considered so.

The values of the microarthropods in the F_1 layer and those of the macroarthropods in the A_1 layer are not inserted since comparable values of other groups fail. The greatly diverging densities of the different groups and species compelled us to indicate the densities of some groups with columns of double, three-, four- or even tenfold widths; the data of the average densities are given above the columns here. Solid columns indicate predominantly saprophagous and fungivorous groups, cross-hatched columns refer to species with predominantly carnivorous habits.

It appears from the diagram that the densities of the microarthropods and the macrofauna expressed in numbers resp. per 40 cm³ and per 40 dm³ vary in about the same range. So the numbers in the same volume unit differ a factor 1000. Only the nematodes occurred in much larger numbers. It should be remembered that these samples were taken at one point of time only and that no separate species are identified in this group. This is, however, also the case with tardigrads and rotifers. No separate species were distinguished too in some smaller groups of the microarthropods and the hemiedaphic macrofauna (Parasitidae, Trombidiformes, Poduromorpha excl. of *Hypogastrura armata* and *Onychiurus armatus*, Staphylinidae and Araneina). For comparison the density of all Oribatei together is also given. Of the seasonal geophiles only the Anthomyidae larvae appear to occur in a very large density. The epedaphic fauna has only small densities, which was to be expected because of the rare occurrence of the species in the samples of 4 dm³.

The high densities of the macrofauna species living predominantly carnivorously are striking. It seems probable that a large part of these species, belonging to the smallest representatives of the macrofauna, prey on species of the mesofauna. Of the mesofauna only the Parasitidae and the Trombidiformes, occurring in a relatively low density live for the greater part carnivorously.

The numbers of individuals, as they are given in fig. 15, only show one aspect of the densities of the species. If we multiply the

mesofauna figures with 1000 we get an insight into the ratio of the absolute numbers. In relation to our purpose — a survey of the animal floor community in quantitative respect — it is also of importance to compare the biomass of the species mutually. Its value is expressed as the total volume of animal substance per species in thousandths of a mm^3 per 40 cm^3 (in the case of mesofauna) and in mm^3 per 40 dm^3 (in the case of macrofauna): the population volume.

The calculation of the population volume is made by multiplying the average volumes of the bodies of the juvenile stages and the adults, by the numbers in which they occur in 40 cm^3 (mesofauna) or in 40 dm^3 (macrofauna).

The individual volumes were inferred from the measurements.

For mites and beetles it was done by multiplying the length of the body (excl. the gnathosome resp. the head) by the product of its average height and width. For the beetles the volume calculated was controlled by plunging the animals in a calibrated measuring glass partly filled with water. The values calculated and determined appear to agree rather well (table 23). Of some types of mites models, a hundred times enlarged, were made and their volume was determined. Here too the values calculated and measured did not diverge more than 10 %.

The volume of collembolus and other long-shaped animals like nematodes, worms, millipedes, fly-, midge- and beetle-larvae was calculated by multiplying the length by the average surface of the cross-section. For some large animals the volume was measured again by plunging, the results of which agreed satisfactorily with the values calculated.

Though this way of determining the volume is not very exact, the results satisfy for the object concerned: the comparison of species of greatly diverging sizes.

In the tables 24 and 25 the results of the calculations are inserted, in fig. 16 (p. 143) they are graphed. These population volumes give quite another impression than the absolute population densities (fig. 15). Differences in form of the body, place in the range of the body sizes and increasing size during the development are the cause of it.

Striking are the great discrepancies in the cases of *Nematoda*, *Dendrobaena* and *Arion*.

The very small population volume of the nematodes is caused by the predomination of the smaller forms and the small individual volumes, which clearly is not compensated by their large numbers.

Very high are the population volumes of *Dendrobaena octaedra* and *Arion subfuscus*. As to the size of these species *Dendrobaena* belongs for the greater part and *Arion* for a small part to the megafauna (length $> 20 \text{ mm}$). So their individual volume is great.

In the F_0 layer *Arion subfuscus*, in the F and H layer *Dendrobaena octaedra* is the predominating species with reference to the population volume. In the F layer *Nothrus silvestris* succeeds it,

Table 24. Population density and population volume of the mesofauna.

	Individual volume in mm ³	F ₀		F ₁		F _x		H	
		Density per 40 cm ³	Volume in mm ³ per 40 cm ³	Density per 40 cm ³	Volume in mm ³ per 40 cm ³	Density per 40 cm ³	Volume in mm ³ per 40 cm ³	Density per 40 cm ³	Volume in mm ³ per 40 cm ³
<i>Nanhermannia elegantula</i> . . .	0.008	0.7	0.006	0.5	0.004	3.6	0.029	0.6	0.005
<i>Hypochthonius rufulus</i> juv. . .	0.004	4.0	0.016	10.8	0.043	11.9	0.048	3.5	0.014
Idem adult . . .	0.015	1.3	0.020	3.1	0.047	1.7	0.026	0.5	0.008
			0.036		0.090		0.074		0.022
<i>Brachychthonius</i> sp. . .	0.001	0.7	0.001	2.5	0.003	12.4	0.012	4.8	0.005
<i>Nothrus silvestris</i> juv.	0.010	7.4	0.074	6.5	0.065	83.6	0.836	37.6	0.376
Idem adult . . .	0.040	1.7	0.043	8.0	0.320	24.4	0.976	3.8	0.153
			0.117		0.385		1.812		0.529
<i>Platynothrus peltifer</i> juv. . .	0.013	5.2	0.068	3.1	0.041	0.5	0.007	0.3	0.004
Idem adult . . .	0.050	2.5	0.125	2.3	0.115	0.8	0.040	—	—
			0.193		0.156		0.047		0.004
<i>Oppia neerlandica</i> ¹⁾ . . .	0.002	4.7	0.010	46.2	0.092	159.3	0.319	75.8	0.152
<i>Tectocephus velatus</i> juv. . .	0.001	0.7	0.001	6.1	0.006	7.9	0.008	1.2	0.001
Idem adult . . .	0.004	0.5	0.002	11.5	0.046	7.2	0.029	0.5	0.002
			0.003		0.052		0.037		0.003
<i>Oribatula tibialis</i> . . .	0.010	1.5	0.015	2.0	0.020	0.3	0.003	—	—
<i>Chamobates schützi</i> . . .	0.009	4.3	0.039	4.7	0.042	0.9	0.008	0.1	0.001
<i>Phthiracarus borealis</i> . . .	0.020	0.5	0.010	1.4	0.028	2.4	0.048	0.2	0.004
<i>Oribotritia loricata</i> . . .	0.030	—	—	1.3	0.039	5.5	0.165	2.5	0.075
<i>Pseudotritia minima</i> . . .	0.003	—	—	0.4	0.001	2.6	0.008	27.4	0.082
<i>Cilliba</i> sp.	0.007	2.7	0.019	9.5	0.067	11.4	0.080	5.5	0.039
<i>Trachytes</i> sp.	0.016	5.3	0.085	6.4	0.102	2.2	0.035	0.3	0.005
Parasitidae	0.042	5.4	0.227	6.8	0.286	7.2	0.302	3.4	0.143
Trombidiformes	0.001	9.2	0.009	35.9	0.036	43.1	0.043	23.7	0.024
Acaridae	0.001	3.7	0.004	8.8	0.009	8.8	0.009	2.1	0.002
<i>Isotoma</i> sp.	0.050	6.4	0.320	16.7	0.935	21.1	0.106	3.0	0.150
Poduromorpha	0.001	3.2	0.003	6.5	0.007	41.5	0.042	41.0	0.041
<i>Hypogastrura armata</i>	0.070	14.5	0.102	24.5	1.715	7.3	0.511	3.0	0.210
<i>Onychiurus armatus</i>	0.080	—	—	2.7	0.216	6.9	0.552	3.2	0.256
Nematoda	0.00007	342	0.024	1160	0.081	1022	0.072	2655	0.182
(av. length 0.4 mm)									
idem (av. length 0.9 mm)	0.00064	21	0.013	53	0.034	8	0.005	61	0.039
			0.037		0.115		0.077		0.221
Rotatoria	0.0003	87	0.026	23	0.007	2	0.001	26	0.008
Tardigrada	0.0009	81	0.073	17	0.015	4	0.004	2	0.002

¹⁾ inclusive other Eremaeidae.

Table 25. Population density and population volume of the hemiedaphic macrofauna.

	Class of size	Dimensions in mm			Individual volume in mm ³	F ₀		F		H		A ₁	
						Density per 40 dm ³	Volume mm ³ per 40 dm ³	Density per 40 dm ³	Volume mm ³ per 40 dm ³	Density per 40 dm ³	Volume mm ³ per 40 dm ³	Density per 40 dm ³	Volume mm ³ per 40 dm ³
		l.	w.	h.									
<i>Dendrobaena octaedra</i> . .	IV	30	2	2	94.2	16	1507	61	5746	19	1790	2	188
<i>Arion subfuscus</i> . .	II	6	2	2	18.8	4	75	7	132	2	38	—	—
	III	12	4	4	150.7	11	1658	9	1356	2	301	5	754
	IV	20	6	6	565.7	11	6223	—	—	1	566	—	—
							7956		1488		905		754
<i>Lithobius calcaratus</i> . .	II	6	0.7	0.5	2.1	—	—	6	13	3	6	3	6
	III	12	1.3	1.0	15.6	1	16	2	31	1	16	—	—
	IV	20	2.2	1.8	79.2	—	—	1	79	—	—	—	—
							16		123		22		6
Geophilidae . . .	II	6	0.2	0.2	0.2	—	—	3	1	31	6	25	5
	III	12	0.4	0.4	1.5	—	—	9	14	79	119	37	56
	IV	20	0.7	0.7	7.7	—	—	6	46	21	162	110	847
							—		61		287		907
<i>Cylindrojulus silvarum</i> . .	I	3	0.4	0.4	0.4	—	—	11	4	22	9	—	—
	II	6	0.8	0.8	3.0	7	21	21	63	35	105	10	30
	III	12	1.2	1.2	13.6	—	—	11	150	22	299	7	95
	IV	20	1.8	1.8	50.9	2	102	9	458	16	814	5	255
							123		675		1227		380
Incurvariidae . .	II	6	1	1	4.7	3	14	46	216	7	33	3	14
Staphylinidae larv.	I	3	0.25	0.25	0.15	44	7	49	7	52	8	5	1
	II	6	0.5	0.5	1.2	24	29	39	47	36	43	18	22
	III	12	1	1	9.4	2	19	5	47	9	85	3	28
	IV	16	1.3	1.3	21.2	—	—	—	—	2	42	7	148
							55		101		178		199
Staphylinidae im.	I	3	0.7	0.4	0.8	21	17	155	124	33	26	12	10
	II	6	0.8	0.7	3.4	11	37	41	139	36	122	12	41
	III	12	1.8	1.0	21.6	—	—	6	130	11	238	—	—
							54		393		386		51
Cantharidae larv.	I	3	0.4	0.4	0.4	4	2	92	37	64	26	27	11
	II	6	0.7	0.7	2.3	2	5	29	67	19	44	8	18
							7		104		70		29
<i>Athous subfuscus</i> larv.	I	3	0.25	0.25	0.15	1	0.2	3	0.5	74	11	53	8
	II	6	0.6	0.6	1.7	—	—	20	34	142	241	62	105
	III	12	1.4	1.4	18.5	1	18.5	26	481	38	703	6	111
							19		516		955		224
<i>Fannia spec. larv.</i> .	II	6	2	1	12	10	120	14	168	3	36	2	24
<i>Obisium muscorum.</i>	I	3	1	1	2.4	22	53	11	26	3	7	—	—

	Class of size	Dimensions in mm			Individual volume in mm ³	F ₀		F		H		A ₁	
						Density per 40 dm ³	Volume mm ³ per 40 dm ³	Density per 40 dm ³	Volume mm ³ per 40 dm ³	Density per 40 dm ³	Volume mm ³ per 40 dm ³	Density per 40 dm ³	Volume mm ³ per 40 dm ³
		l.	w.	h.									
Araneina . . .	0	2	0.6	0.6	0.55	23	13	104	57	122	67	63	35
	I	3	1.0	1.0	2.35	52	122	66	155	73	172	58	136
	II	6	2.0	2.0	18.8	8	150	2	38	9	169	2	38
	III	8	2.6	2.6	42.5	3	128	1	43	—	—	—	—
							413		293		408		209
<i>Rhagio lineola</i> larv. I—VIII	III	9	1.3	1.3	11.9	4	48	32	381	49	583	40	476
<i>Phaenocladus</i> sp. larv. XII—V	I	3	0.25	0.25	0.16	167	27	31	5	11	2	16	3
Anthomyidae larv. XII—III	II	5	1	1	3.9	341	1330	230	897	18	70	—	—
Pentatomidae VIII-III	II-III	7	4	2	56	10	560	15	840	3	168	3	168

which surpasses the more numerous *Oppia neerlandica* because of its larger size.

The species of the hemiedaphic macrofauna, living predominantly carnivorously, appear to possess a relatively small population volume and a relatively large population density. In the carnivorous epedaphic beetles and spiders it is quite the reverse: their population density is very small, their population volume is rather large.

For the stability in the community a right proportion of the predacious elements to those feeding in another way is very important. The groups of predators have a rather low population volume compared with the saprophages. In the community of the floor, which may be considered as a rather stable one, the predators probably form, together with other factors, a sufficient check against a stronger development of the non-predacious groups.

CHAPTER VI

IMPORTANCE OF THE FOREST FLOOR FAUNA FOR THE DECOMPOSITION OF THE LITTER

The multiform composition of the soil fauna implies that the part played by it in the decomposition of the litter is very complex. The way of living, the life cycle and the variations in population density are still very insufficiently known, even of the most important species. What is known, however, of some groups such as earthworms and millipedes gives some notion of the importance of these groups in this respect. The influence of the soil fauna on the substrate is to be attributed to processes related to locomotion and those related to metabolism.

With regard to locomotion, especially movements in the mineral soil are important. The passages formed enlarge the aeration of the soil and influence its water management. Moreover these movements cause a mixing of organic and inorganic material, which highly benefits the activity of the microorganisms (WITTICH 1939, 1943).

In forests on poor soils, generally showing a slow decomposition of the litter, the whole mesofauna stays in the A_0 layer and only some macrofauna species occur in the upper layers of the mineral soil. So the influence of the animal movements is mainly restricted to aeration of the organic layer. In this respect the importance of the species will be dependent on their mobility and will vary for each species. An investigation into this matter in natural circumstances is not possible. In this respect we are obliged to observe animals in cultivation under circumstances as natural as possible. Nematodes in general are very mobile. Of the Oribatei especially the Malaconothridae (*Nothrus*, *Platynothrus*, *Hypochothonius* a.o.) and the Phthiracaridae (*Oribotritia*, *Pseudotritia*) are slow animals. *Oppia* species, however, are very mobile. Also mobile are the preying Parasitidae and Trombidiformes, and the predominantly saprophagous Poduromorpha. *Dendrobaena octaedra* lies motionless for hours in culture dishes, but is able to move very quickly if disturbed. *Cylindrojulus silvarum* generally moves rather slowly in contrast to *Julus scandinavicus*, which is very mobile. All predacious macroarthropods move quickly: centipedes, staphylinids, larvae of Cantharidae, spiders, false scorpions and predacious fly larvae (*Rhagio lineola*). Saprophagous wireworms and fly larvae generally move little and slowly.

Also the sizes of the animals determine the effect of the movements in some respect: only when these sizes exceed those of the interstices in the litter layer, the movements will influence its aeration. Consequently the movements of the mesofauna will be of little or no importance in a raw humus soil, those of the macrofauna are most important in the layers with the densest structure: F_x and H layers.

The processes related to metabolism and their intensity are of the highest importance in defining the influence of the fauna on the substrate. Metabolism itself is to be studied by means of the consumption of oxygen and the evolution of carbondioxyde, while from these data the respiration quotient (the ratio of the volume CO_2 evolved to the volume O_2 consumed) can be deduced which gives some indication of the nature of the substances utilized. In the complete combustion of carbohydrate the respiration quotient is 1.0, for fat and protein (when oxidized only as far as uric acid) it is about 0.7 (WIGGLESWORTH 1947).

BORNEBUSCH (1930) made an investigation into the respiration of the soil fauna. With the aid of KROGH's microrespiration apparatus he ascertained the oxygen consumption of 25 specimens belonging to 19 common forest soil species of greatly diverging size (worms, Collembola, Carabidae, Staphylinidae, Diptera larvae,

spiders etc.). Applying the surface law to these results, respiration proved to vary between 0.08 and 0.23 mg O_2 per hour per gram-individual. BORNEBUSCH thinks these data sufficiently conformable to apply the average, 0.14 mg O_2 per gram-individual per hour at $13^\circ C$, to all species and groups. From this empirical statement and the average weights fixed for each species BORNEBUSCH calculated respiration values specified as mg O_2 per hour for $1 m^2$ at $13^\circ C$. Using these values for a comparison of the different soil types he found that the best mull soils obtain the most intensive animal life; these are followed by the raw humus soils, the intensities in which are a little above that in the Melica mull and greatly exceed the intensity in the Oxalis mull and in the deteriorated soil. The relatively high respiration value in the raw humus soils must be ascribed to the large numbers of the microarthropods and those of Diptera- and Elateridae larvae in this type. The large number of microarthropods, which only little increase the total weight of the fauna have a considerable oxygen consumption (20-30% of the total). If we consider, moreover, that a large number of the smaller microarthropods are not inserted in consequence of the investigation technique applied (see p. 11) it is obvious that these animals play an important part in the processes of life in the raw humus floor. In order to ascertain an absolute value for the oxygen consumption during a year the ratio between the O_2 consumption at the average temperatures of the different months and the consumption at $13^\circ C$ was determined. This was done with the aid of the temperature metabolism curve of KROGH (1914). This curve was, however, made for the metabolism of vertebrates, the central nervous system of which was eliminated. According to ELLINGER (1916) this curve also applies to gnats in diapause. Supposing this curve of KROGH is appropriate to the respiration of his soil animals — "which were examined in a state of relative inaction, alone and without food in the experiment glasses, where they could move about at pleasure, but without receiving any impulses from without" — BORNEBUSCH is of opinion that the respiration values he arrived at through his calculations constitute minimum values which are not far removed from the maximum values. In this way he comes to an annual oxygen consumption varying between 93 and 18 g O_2 per m^2 in the different forest types. Since the quantity of the litter annually falling is about 400 g per m^2 and a rather equal quantity of oxygen is required for the combustion of the humus material, he concludes to a considerable contribution of the fauna to the decomposition of the litter. Including the Protozoa and the Nematoda, not examined in this study, he values the quantity of organic matter consumed by the metabolic processes of the fauna to be one fifth to one fourth, or perhaps still more, of the total combustion of matter.

It is obvious that the last estimations in particular are based on too many suppositions and approximations to be of much value. So it is assumed in the last conclusion that all soil fauna

species feed on litter or humus material and this is certainly not true: many species feed partly or even wholly on soil fungi etc. However, this study clearly demonstrates the importance, the possibilities and limitations of an investigation in this direction.

Also ULRICH (1933) performed calculations based on the results of his quantitative investigation in order to determine the consumption of the forest soil fauna quantitatively. He starts from the theoretical views of PÜTTER (1911) in his "Vergleichende Physiologie", which have only partly been tested on experiments. PÜTTER based his considerations on organisms with a dry matter content of 15%, which take food with an oxygen capacity of 1.2, i.e. 1 g food is completely combusted with 1.2 g of oxygen. The organisms are globular, exchange food and gases over their whole surface and consume 500 mg of oxygen per m² per hour. From these data PÜTTER calculated for organisms with a volume of 1 μ^3 , 10 μ^3 , 100 μ^3 , ... etc. up to 100 dm³ the daily food consumption (dry matter) in percentages of their own dry weight. For organisms with the volumes mentioned this is resp. 30300, 14000, 6520..... down to 0.065%. PÜTTER compared the consumption calculated and observed in six species and found some agreement in three species only. Nevertheless ULRICH applies the percentages of food consumption calculated by PÜTTER without any restriction. The following objections must be raised to this. In calculating the daily absolute food consumption ULRICH applies PÜTTER's percentages, referring to dry weight, to the volumes, which would only be allowed if both the specific gravities and the water contents of the food on the one side and the different animals on the other side, were the same. Further he does not take the nature of the food into account (so he takes for granted an oxygen capacity of 1.2), neither the fact that only part of this food is really combusted. Hence, in my opinion, the total food consumption of the soil fauna, calculated by him is of no value. That these data really lead to untenable conclusions appears from ULRICH's estimation that the soil fauna present in a 6-8 cm high humus layer of a spruce forest would completely decompose this organic matter in $3\frac{1}{3}$ year. If, besides, we take into consideration that the numbers of mites and collembolus — the most important consumers according to his calculation — are rather low, in consequence of the technique applied, it is obvious that here a completely wrong result is got, highly overrating the contribution of the fauna to the decomposition of the litter because of a misapplication of the considerations of PÜTTER.

Next to these calculations ULRICH made also some decomposition experiments in pots. Litter samples from which the fauna had been removed, samples with a normal fauna, and samples with a fauna density five times enlarged, were kept in circumstances as natural as possible during $1\frac{1}{4}$ year. After this period the fauna was analysed and appeared to possess almost the same density in all samples. In the normal samples the density had decreased

with 50-70%, in the samples overpopulated with almost 90%. The chemical analysis of the litter material showed a distinct decrease of crude fibre and a still larger decrease of the other organic materials. The differences found between the contents of crude fibre in the litter samples with different fauna densities are too small to consider them as significant with this extent of the material. Direct influence of the fauna on the decomposition of the litter is not proved by them. The important part, which the different mould species play in the decomposition of these materials is not mentioned at all.

In which way SOUDEK (1928) tried to gain an insight into the significance of the soil fauna in respect to the decomposition of the litter was already mentioned in the survey of the literature. He took it for granted that in any soil fauna species the quantity of food passing daily the digestive tract is equal to twice the contents of the intestinal canal. No arguments are adduced to prove this supposition and it seems improbable in its generality.

BORNEBUSCH, ULRICH and SOUDEK tried to gain an insight into the significance of the fauna for the decomposition of the litter in an indirect way. BORNEBUSCH succeeded in comparing the fauna and its intensity of metabolism for different forest types mutually. The absolute values, which BORNEBUSCH calculated for the metabolism, and ULRICH and SOUDEK for the litter consumption are, however, unsatisfactory.

The only way to get data in regard to the influence of the fauna on the decomposition of the litter in a more direct way is by rearing species on well-known litter material under controlled circumstances.

In this way LINDQUIST (1941) made investigations with earthworms and slugs. FRANZ and LEITENBERGER (1948) observed several soil fauna species: earthworms, isopods, millipedes, Diptera larva etc. These last investigations are of utmost importance: the litter consumption was examined quantitatively and the degree of decomposition of food and excrements was determined.

FRANZ and LEITENBERGER started from litter newly fallen, on which a certain number of individuals of one species was reared. From their data it appears that the consumption of new litter is very small. In order to get sufficient excrements for a chemical analysis the experiments had to be continued for several weeks or even months. The degree of decomposition was determined with the method of SPRINGER: only truly humified substances do not dissolve in acetyl bromide. The carbon in this insoluble fraction (C_h) expressed in % of the total carbon (C_t) constitutes the "Zersetungsgrad", the decomposition rate. In these experiments the values of the decomposition rate for excrements were considerably higher than those for food (litter). This fact seems to prove that organic material passing the intestinal canal is humified. However, in these experiments it is not taken into account that the excrements were exposed to the influence of microorganisms for

weeks and months. The increase in the decomposition rate may be — at least partly — a consequence of the attack of microorganisms. An indication of this supposition may be the low degree of decomposition of excrements of locusts, reared on fresh material of the grass *Dactylus glomeratus* and clover *Trifolium pratense* for 6 days only. In both cases the values of the decomposition rate of the excrements were only a little higher than those of the food material.

The data of the litter consumption presented in mg per day per individual do not give a right impression of the quantity of litter consumed by the different species in nature. It must be objected that the animals were fed on litter newly fallen. According to my experience the greater part of the species is only found in small density in the upper litter layer and also excrements of these animals are scarcely observed there. So it seems probable to me that the litter newly fallen is not the natural food of these animals and it is only eaten in cultures for want of something better. Our cultures with *Cylindrojulus silvarum* (p. 110 table 20) on F_0 material showed a slower growth and a greater mortality than on F_x material. F_0 was consumed in considerably smaller amounts than F_x . This affirms the supposition that F_0 is not the adequate food of this species. Similar results we got with *Julus scandinavicus*, *Glomeris marginata* and *Dendrobaena octaedra* (see p. 158 table 30). The values calculated by FRANZ constitute only minimum values, the values might have been much higher if choice of food had been possible.

It is striking in the results that the difference between the quantity of organic material ingested and the quantity of excrements defecated during the same time is very large. This difference in hundredths of the food ingested, the retention percentage, was about 50. Our own experiments discussed below, in which *Glomeris marginata* was reared on older litter for 5 days, showed a retention of about 5% of the food ingested. Perhaps this large difference in retention may partly be explained in the same manner as the increasing decomposition rate in the same experiments: in consequence of attack by microorganisms during several weeks the excrements have decreased in weight. It is not impossible, however, that with a very slow passage of the food through the digestive tract, caused by a small ingestion of unsuitable food, a larger part of the food is utilized than with a quick passage.

Our own investigation into the direct influence of the fauna on the decomposition of the litter concerns two questions:

1. Which changes does the litter undergo if taken as food by a certain species and in which degree are the chemical components of it used in the upbuilding of the body substance resp. utilized in metabolic processes?

2. In which quantity is the litter consumed and converted into excrements?

To be able to answer these questions rearing tests in vitro are necessary. Not all species are easily kept alive in culture circum-

stances. Millipedes offer fewest difficulties: they can be kept alive for quite a long time on one year old litter without any noticeable mortality. Contrary to the experiences of FRANZ and LEITENBERGER (1948) it appeared unnecessary in cultures of these animals to have a sand layer under the litter at the bottom of the culture dish if the litter was moistened to such a degree that all the water was absorbed by the litter material. After desiccation, in order to remove the animals present, the litter material was selected as homogeneous in composition as possible and was cut into pieces of about $\frac{1}{2}$ cm². Water was added to an amount of 200% of the air-dry weight, the water content being about 230% of the absolute dry weight or 70% of the total weight. Before the animals were released in this litter they were first kept in an empty petri-dish for 24 hours, in which they emptied their intestinal tract. At the end of the culture period, which lasted at most 5 days in order to prevent attack of the excrements by moulds, the animals were again isolated and the excrements produced during 24 hours were added. Excrements and food rests could be separated exactly by sieving the material desiccated.

To get an insight into the first question, experiments were made with a species which did not occur in the beech forest investigated, but which was rather numerous in a neighbouring oak forest: *Glomeris marginata* Vill. This species, the largest of the millipedes occurring here, ate the largest quantity of litter and could be collected in sufficient numbers to get in some days the quantity of excrements required for a chemical analysis. This analysis was made by the State Agricultural Experiment Station, Maastricht and concerned the contents of nitrogen, phosphor and calcium of the food material, food rests and excrements.

The experiment was made in the following way: 264 animals weighing 30.5 g together were released after defecation of their pre-experiment intestinal contents in 20.000 g oak litter F₁ (air-dry weight at R. H. 55%) to which was added 40 cm³ water. After a culture period of three days at room temperature (18° C) the animals were removed. After adding the excrements of the next 24 hours the material was separated into excrements and food rests. Finally these two parts were weighed at the same relative humidity as the original material had, and sent in to be analysed. The contents of the materials concerned and the quantities calculated appear from table 26.

The results of the analysis of nitrogen and P₂O₅ were accurate within a range of + and - 0.025% (second decimal place rounded at 5 or 0), those of CaO within a range of + and - 0.05% (first decimal place rounded at whole figures) so that the quantities calculated from them lie between the ranges indicated. The quantities consumed are calculated by subtracting the foodrest from the quantities of food. The quantities utilized i.e. converted into body substance or combusted at metabolism are got by subtracting the quantities eaten and the excrements. Though the

Table 26. Some chemical substances utilized by *Glomeris marginata* reared on oak litter (F₁).

	Air-dry weight in mg	Nitrogen % mg	P ₂ O ₅ % mg	CaO % mg
Food	20000	2.55 510 ± 5	0.35 70 ± 5	1.1 220 ± 10
Foodrest	8547	2.60 222 ± 2	0.35 30 ± 2	1.1 94 ± 4
Consumed	11453	288 ± 7	40 ± 7	126 ± 14
Excrements	10735	2.50 268 ± 3	0.30 32 ± 3	1.0 107 ± 5
Utilized	718	20 ± 10	8 ± 10	19 ± 19
Quantities utilized in % of quantities consumed (retention %)	6	7 (4-10)	20 (0-36)	15 (0-27)

contents of the chemical constituents examined in food and excrements only differ little, at least the quantity of nitrogen utilized appears clearly demonstrable. The quantities of P₂O₅ and CaO utilized are less clear. This is caused by the lower contents of these materials and (especially in the case of CaO) by the small accuracy of the analysis results. However, the possibility to demonstrate the consumption of these elements is only annulled by the most unfavourable combination of rounding.

The results obtained in a corresponding experiment with the same species and the same litter are presented in table 27. In

Table 27. Percentages of some chemical substances in food material (oak litter, F₁), excrements of *Glomeris marginata*, reared on this material and dry body substance of this species.

	Nitrogen %	P ₂ O ₅ %	CaO %
Litter (air-dry)	2.20	0.30	1.10
Excrements (air-dry) . .	2.25 (2.10)	0.25 (0.25)	1.00 (0.95)
<i>Glomeris marginata</i> (dry body substance 105° C)	6.60	1.00	3.60

this experiment the retention was 7% of the food consumed. To compare the absolute quantities of nitrogen, phosphor and calcium in food and excrements the percentages of the excrements must be multiplied by 0.93. These values are placed in parentheses. Here, too, about 5% of the nitrogen and about 15% of the phosphor and the calcium, present in the food, appear to be utilized.

If we compare the contents of N, P and Ca in the dry body substance of *Glomeris* to those in the litter (in which case the latter have to be raised with $\frac{1}{9}$ because of the water content of 10% in the litter) it appears that nitrogen, phosphor and calcium are concentrated about three times in the body substance. The

proportion of the nitrogen, phosphor and calcium contents of the body substance does not agree with the absolute quantities absorbed as these were calculated in the preceding experiment. Comparatively less phosphor and calcium are present in the body substance than nitrogen. The explanation is probably to be found in a greater loss of phosphor and calcium in moulting. There was not sufficient material available to analyse the skins cast.

The excrements got in cultures of *Glomeris marginata* — like those of other millipedes, fly larvae and earthworms — appeared to consist in particles of litter with a surface of about 0.01 mm². In examining them microscopically they still clearly showed reactions of cellulose and lignin. So a priori it did not seem probable that the degree of decomposition was considerably increased in passing the intestinal tract. The large differences in decomposition rate, which FRANZ and LEITENBERGER found between litter and excrements, however, induced us to examine litter and excrements of *Glomeris marginata* in a corresponding way. Dr F. C. GERRETSEN, head of the Microbiological Department of the Agricultural Experiment Station and Institute for Soil Research T.N.O., Groningen, kindly made some analyses. Examined was oak litter (F₁) and excrements, produced from this material by *Glomeris marginata* in 5 days.

The contents of carbon and nitrogen in the whole material (C_t and N_t), those of carbon and nitrogen in "humus" fraction (insoluble in acetylbromide, C_h and N_h) and the ash contents, all of them in percents of dry matter, are given in table 28

Table 28. Percentages of carbon and nitrogen in F₁ oak litter and in excrements of *Glomeris marginata* fed on it (C_t and N_t), percentages of these substances in the "humus" fractions of these materials (C_h and N_h) and the ash contents of the same (duplo analyses).

	Litter		Excrements	
C _t	46.0	46.2	45.3	45.3
N _t	2.3	2.3	2.3	2.3
C _h	12.8	12.0	11.4	11.0
N _h	1.05	1.1	0.93	0.95
Ash	7.5	7.3	8.95	8.9

(analyses in duplo). The higher ash contents in the excrements are supposed to be attributable to dust falling on the excrements in desiccating. If the contents are calculated on ash-free matter the differences between the C_t contents disappear, the N_t contents remain the same, C_h and N_h remain somewhat lower in the excrements than in the litter. From the data presented the decomposition rate, $\frac{100 C_h}{C_t}$, was calculated at 25.2 (excrements) and 27.8 (litter). If calculated from the contents in ash-free matter the

decomposition rates keep about the same values. If the difference of these two figures is significant, there is a slight decrease instead of an increase of the decomposition rate of the litter in passing the intestinal tract. This may be explained by a slight absorption of carbon and nitrogen out of the humus fraction of the litter. An increase of the decomposition rate as it was determined by FRANZ and LEITENBERGER is out of question here. This is in accordance with the microscopic investigation of the excrements.

From these results it may be concluded that *Glomeris marginata* is only of little significance in the chemical breakdown of the litter. Its main significance is to be seen in the diminution, the mechanical breakdown, of the litter material. However, this may be very important. The small quantities of foodstuffs taken from the ingested litter are probably the cause that a great amount of litter has to be consumed for the fulfilment of the food requirements. The large quantities of excrements resulting from this are attacked much more easily by microorganisms, especially saprophytic fungi, than the not eaten litter. Mechanical breakdown — though in itself not important in the decomposition process — promotes decomposition by favouring attack by microorganisms.

On account of the composition of the excrements it seems probable to me that the majority of the soil fauna acts in the same way with regard to the breakdown of the litter. Only in some soil fauna species (*Lamellicornia* larvae, *Tipulidae* larvae, BUCHNER 1930) symbiotic microorganisms capable of breaking down cellulose are known. More detailed investigations into the digestion of soil fauna species — including mesofauna species — are necessary to support the view mentioned above.

The quantity in which litter is consumed is dependent on animal species, kind of litter, moisture content of the food and temperature.

The influence of temperature and moisture on the litter consumption in the case of *Glomeris marginata* may be deduced from table 29. In these experiments ten mature individuals of the same size were reared during 5 days on F₁ oak litter at different temperatures and water contents of the food material. Only the excrements were weighed in these experiments, but as was seen above the amount of excrements defecated is roughly proportionate to the amount of litter consumed. It seems that during a short time of rearing the optimal temperature is between 17.5 and 22.5° C and the optimal water content of the food is about 70%. This range of optimal temperature was affirmed by experiments during a longer time (4 months) at constant temperatures. Defecation (and consumption) decreased at all temperatures investigated but remained relatively highest at about 19° C (17.5-21° C). At this temperature also the mortality during these 4 months was lowest.

The extent of the consumption of litter by different saprophagous species may appear from rearing tests executed under the same circumstances as to temperature and moisture. Table 30 gives the results of cultures, simultaneously performed with 10

Table 29. Excrements of 10 mature individuals of *Glomeris marginata* reared during 5 days on oak litter (F₁) under different conditions of temperature and water content (experiments in triplo).

Temperature °C	7	13	17.5	22.5	27
Excrements in mg (air-dry) (water content 70 %)	220	648	872	969	576
	295	623	790	1008	809
	216	501	1189	939	694
	Average	244	591	950	972
Water content in % of total weight idem in % of air-dry weight	10	55	70	82	90
	0	100	200	400	800
Excrements in mg (air-dry) (temperature 18 °C)	15	640	850	815	635
	20	410	1030	680	715
	30	560	1010	930	930
	Average	22	537	963	808

mature individuals of some saprophagous species on different litter. To eliminate the size of the species the consumption of litter (water content 70%) was expressed in percents of the fresh body weight, which varies only little in the same species under the experimental circumstances. The values given show distinctly that F₀ material is only very little eaten, especially that of red oak and Scotch pine. It is striking that the F₁ litter of the same tree species is eaten in the largest quantities. The values given for the worm *Dendrobaena* are of little value. Contrary to the others, this species is difficult to keep alive on litter without a sand layer. The normal litter consumption is supposed to be higher.

As was already mentioned these tests were executed with mature individuals of which those of the same species were of about the same size. This is necessary since the consumption of small individuals in ratio to their body weight is a good deal larger than that of large individuals. In table 31 the results are given of experiments with *Glomeris marginata*. Nine tests, each with ten individuals of the same size, were performed on oak litter (water

Table 30. Daily litter consumption in percents of the body weight.

	Average ind. weight in mg	F ₀				F ₁			
		Beech	Oak	R. oak	Sc. Pine	Beech	Oak	R. oak	Sc. Pine
<i>Julus scandinavicus</i> . . .	60	8	8	3		16	22	31	17
<i>Cylindrojulus silvarum</i> .	60	12	7	1	3	33	29	40	43
<i>Glomeris marginata</i> . .	150						26		
<i>Tipula scripta</i>	60					42			
<i>Dendrobaena octaedra</i> .	350	1				10			

Table 31. Litter consumption of *Glomeris marginata* of different sizes.

Average ind. weight in mg (w)	Daily litter consumption in % of body weight	Litter consumption in mg air-dry material per ind. per 5 days (c)	$\sqrt[3]{w^2}$	$\frac{c}{\sqrt[3]{w^2}}$
51.2	70	60.0	13.8	4.3
52.9	62	54.4	14.1	3.9
52.2	66	58.8	14.2	4.1
114.7	49	94.2	23.6	4.0
116.4	46	88.5	23.8	3.7
122.1	52	104.8	24.6	4.3
185.5	33	100.8	32.5	3.1
186.5	43	133.2	32.6	4.1
199.8	32	107.4	34.2	3.1

content 70%, 18° C) during 5 days. The three groups differing in size show clear differences in relative litter consumption. For the smallest individuals it is about twice that of the largest ones.

If we take the consumption as an indirect measure of metabolism we might expect — according to the surface law — the litter consumption per individual in each size to be proportional to the active surface. Since large and small individuals completely agree in form the surfaces bear the proportion of $\sqrt[3]{w^2}$ (w = weight). In fact it appears that the ratio between the litter consumption and $\sqrt[3]{w^2}$ (and so to the active surface) only diverges little in 7 out of 9 cases. For the largest individuals the ratio is distinctly lower in two cases. Perhaps the explanation is that in consequence of age, metabolism and consequently litter consumption diminished.

Similar results were obtained with a culture of *Cylindrojulus silvarum* on beech litter (F_1): table 32. Here, too, we find with an increasing weight a strong decrease in the litter consumption in percents of the body weight. Except for the largest animals the litter consumption per individual is again fairly proportional to the active surface. In comparison with the values of the litter consumption of the mature animals given in table 29 the consumption of the largest individuals in this test is very low. Probably this is to be ascribed to a fluctuation in the food consumption during the year. The results of table 29 refer to experiments in the beginning of June, culture tests with individuals of different sizes were performed in January. Also with *Glomeris* indications were found for a seasonal fluctuation in the consumption.

This circumstance makes it impossible to calculate the total annual litter consumption from the values found for the litter consumption of the different stages at various temperatures and moisture and their average densities in a certain area.

From the foregoing it may be evident that an extensive investigation into the seasonal fluctuation and the influence of

Table 32. Consumption of beech litter by *Cylindrojulus silvarum* of different sizes.

Length in mm	Average ind. weight in mg (w)	Daily litter consumption in % of body weight	Litter consumption in mg air-dry material per ind. per week (c)	$\sqrt[3]{w^2}$	$\frac{c}{\sqrt[3]{w^2}}$
7	3.4	51	3.9	2.2	1.8
9	6.9	37	6.0	3.6	1.7
18	25.7	29	17.7	9.0	2.0
25	68.5	9	14.7	16.8	0.9

temperature and moisture on the litter consumption has to be made before an exact quantitative insight into this matter can be gained.

SUMMARY

In this paper a description on quantitative basis is presented of the fauna inhabiting the organic soil layers (floor) of a beech forest without any undergrowth on a poor sandy soil. The most important quantitative investigations on forest soil fauna are briefly reviewed. The methods applied in soil fauna investigations are discussed.

The fauna is discerned in several size groups of which the mesofauna (0.2-2 mm) and the macrofauna (2-20 mm) are studied with respect to their vertical dispersal, horizontal dispersal and seasonal fluctuations.

In the case of the mesofauna the samples for investigation had a volume of 40 cm³ and were taken from the floor layers, separately distinguishable: the upper loose litter layer of the last autumn (F₀), the litter layer of the preceding autumn (F₁), the older litter layers (F_x) and the humus layer (H). For microarthropods (Acari, Collembola) these samples were desiccated slowly in a Tullgren apparatus, the effectiveness of which method was checked. Only some sample series were examined for Nematoda, Rotatoria and Tardigrada by immersing the samples in water.

The macrofauna was studied in samples of 4 dm³ (hemiedaphic macrofauna). These samples were taken from the upper loose litter layer (F₀), the older litter layer (F), the humus layer (H) and the upper mineral soil layer (A₁). To these samples also Tullgren's desiccation technique was applied and its effectiveness for several groups was checked. For part of the macrofauna, occurring in too small density for this method and moving actively on the soil surface e.g. Caribidae, Lycosidae, (epedaphic macrofauna) a trap technique was used. By applying the Lincoln-index method the density of the most numerous species could be estimated.

Data on vertical dispersal are based on catchings throughout the year. In the case of microarthropods the influence of frost and drought on vertical dispersal could be stated. The horizontal dispersal of most microarthropods appeared homogeneous if ex-

pressed as frequency percentages; the densities, however, varied often considerably from spot to spot. Horizontal dispersal in separate epedaphic species was quite different: some species occurred in local concentrations, other were rather homogeneously distributed. Seasonal fluctuations of microarthropod species varied highly and were caused mainly by the juvenile stages. In one species, *Nothrus silvestris*, a more detailed — though still incomplete — analysis of the fluctuations was made. In hemiedaphic macrofauna species phenological and developmental data were recorded. Catching fluctuations of epedaphic macrofauna inform about time of activity (seasonal and diurnal), aestivation, hibernation, hatching of adults and influence of weather conditions on activity.

In all sections the general part is followed by a special part recollecting data from this and other investigations on the different species.

The whole community is represented in two diagrams the first with respect to the absolute density, the second with respect to the biomass, the population volume. The main differences of these representations are discussed.

The importance of the forest floor fauna for the decomposition of the litter is reviewed. The main literature on this subject is discussed and own methods and results mainly with respect to millipedes are presented. It is concluded that the significance of the macrofauna in the forest soil is chiefly to be seen in the mechanical breakdown of the litter. The difficulties in determining the actual contribution in the breakdown of a given species in certain density are stressed.

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APPENDIX

Table A: The numbers of the main microarthropod species caught in 40 cm³ samples from the floor of the beech forest 8 G on the dates indicated.
j. = juvenile, a. = adult; — = samples not taken.

Table B: The numbers of the main macrofauna species caught in 4 dm³ samples from the floor of the beech forest 8 G on the dates indicated.
— = samples not taken.

Table C: The same data as in table B, arranged according to size classes.
— = no animals present in the sample.